ISSN 0704-3716

Canadian Translation of Fisheries and Aquatic Sciences

No. 5385

Sex differentiation in fishes

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Original title: Differentsirovka pola u ryb

In: Izdatel'stvo Leningradskogo Universiteta (University of Leningrad Publishing House). Monograph 12D, p. 67-147, 1975

Original language: Russian

Available from:
Canada Institute for Scientific and Technical Information
National Research Council
Ottawa, Ontario, Canada K1A 0S2

1988

131 typescript pages

NOTE: p. 1-66 are available as Fish. Mar. Serv. Transl. Ser. 4069

Secretary of State / Secrétariat d'État

90-01516/

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU BUREAU DES TRADUCTIONS

LIBRARY IDENTIFICATION – FICHE SIGNALÉTIQUE

Translated from - Traduction de	Into - En
Russian	English

Author - Auteur

Persov, G.M.

Title in English or French - Titre anglais ou français

Sex differentiation in fishes

Title in foreign language (Transliterate foreign characters)
Titre en langue étrangère (Transcrire en caractères romains)

Differentsirovka pola u ryb

Reference in foreign language (Name of book or publication) in full, transliterate foreign characters.
Référence en langue étrangère (Nom du livre ou publication), au complet, transcrire en caractères romains.

Izdatel'stvo Leningradskogo Universiteta

Reference in English or French - Référence en anglais ou français

Leningrad University Press

Publisher - Éditeur	DATE OF PUBLICATION / DATE DE PUBLICATION			Page Numbers in original / Numéros des pages dans l'original
Same	Year / Année	Volume	Issue No. / Numéro	67-147
Place of Publication / Lieu de publication				Number of typed pages / Nombre de pages dactylographiées
Leningrad, USSR	1975	–	12D	129

Requesting Department / Ministère-Client: Fisheries and Oceans

Translation Bureau No. / Notre dossier nº: 3287284

Branch or Division / Direction ou Division: IPB

Translator (Initials) / Traducteur (Initiales): P.J.H.

Person requesting / Demandé par: Dr. E.M. Donaldson

Your Number / Votre dossier nº:

Date of Request / Date de la demande: November 26, 1987

UNEDITED TRANSLATION
For information only
TRADUCTION NON REVISÉE
Information seulement

Canada

SEC 5-111 (84-10)

Secretary of State / Secrétariat d'État

MULTILINGUAL SERVICES DIVISION – DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU / BUREAU DES TRADUCTIONS

Client's No.–N° du client	Department – Ministère	Division/Branch – Division/Direction	City – Ville
	Fisheries and Oceans	IPB	Vancouver
Bureau No.–N° du bureau	**Language – Langue**	**Translator (Initials) – Traducteur (initiales)**	
3287284	Russian	P.J.H.	SEP 14 1988

Source: Izdatel'stvo Leningradskogo Universiteta (University of Leningrad Publishing House), Monograph 12D, pp. 67-147, 1975 (USSR)

U.D.C.597.0/5:591.166

SEX DIFFERENTIATION IN FISHES

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67*

Table of Contents

		Page numbers: Original Text	Translation
Publisher's abstract		2	1
From the author		3	2,3
Introduction		5-9	4-11
Chapter 1.	The Indifferent Period in the Development of the Gonads	10-36	12-59
	Primordial germ cells in the migration period.	11-17	13-26
	Concentration of primoridal germ cells and beginning of gonadal formation.	18-20	26-30
	Transition of primordial germ cells to mitosis.	21-24	30-35
	Changes in the number of germ cells in early ontogeny.	24-35	35-56

*The figures in the right-hand margin are page numbers in the original (Tr.).

UNEDITED TRANSLATION

For information only

TRADUCTION NON REVISEE

Information seulement

SEC 5-25 (Rev. 82/11)

Canada

		Page Numbers: Original Text	Translation
	Formation of oviducts.	36	56-57
	Appearance of fatty tissue in the gonads	36	57-59
Chapter 2.	The Period of Gonadal Differentiation	37-66	58-118
	Indications of anatomical differentiation	37-40	59-65
	Cytological differentiation	41-51	66-90
	Times of differentiation	52-55	90-98
	Natural sex transformation and hermaphroditism	56-63	98-113
	The two basic types of gonadal differentiation	64-66	113-118
Chapter 3.	Development of the Gonads During the First Period After Their Differentiation	67-79	1-23*
	Time frame within which juveniles make the transition to the sea period of life and the rate of development of their gonads	67-69	3-9
	Degree of development of the ovaries in juveniles in the course of catadromous migration	70-75	9-17
	Sex ratios in the young	76-79	17-23
Chapter 4.	Formation of Individual Fecundity During the Period of Early Gametogenesis	80-85	23-32
Chapter 5.	The Early Period of Gametogenesis Under Conditions of Ionizing Radiation	86-102	32-59
	Number of germ cells	86-90	32-40
	Duration of indifferent period	90-92	40-42
	Transition from mitotic cycles to meiotic cycle	92-93	43-65
	Disorders in the hormonal regulation of gametogenesis	94-98	45-52
	Recovery of the structure and function of the gonads	98-102	52-59

*Pagination of translation up to end of Chapter 2 is from Fisheries and Marine Service Translation Series No. 4069. Pagination of remainder of translation (beginning with Chapter 3) will be for Fisheries and Aquatic Sciences Translation Series No. 5385. (Tr.)

	Page Numbers: Original Text	Translation
Conclusion	103-105	59-63
Plates I-XV	133-147	64-78
References	106-132	79- 116

Chapter 3. DEVELOPMENT OF THE GONADS DURING THE FIRST PERIOD AFTER THEIR DIFFERENTIATION

Time frame within which juveniles make the transition to the sea period of life and the rate of development of their gonads

Within the genus Oncorhynchus a trend towards a shortening of the riverine period of life is observed. This is most pronounced in the pink salmon. Consequently, it is precisely in pink salmon that we encounter a falling away of the parr stage. Thus, the smoltification of pink salmon juveniles begins in the absence of the outwardly visible preliminary parr stage, so typical of all the diadromous salmons. At first, it may be thought that the shedding from ontogeny of one of the links of the life cycle is due to changes in the rate of development. The following questions arise: when and in what stages of ontogeny are these changes accomplished, what relation do they bear to the times of sexual maturation and for how long do they persist? The pink salmon also differs inherently from the other far eastern salmons with respect to the number of primordial germ cells (PGCs) with polymorphous nuclei. In some species (the masu, sockeye and coho), more than 90% of the fishes investigated had PGCs with polymorphous nuclei, in others, this was the case with 66.6% (chum) or

slightly less than 42% (pink). The smallest number of such nuclei were encountered in a pink salmon (2.4%), which is from 5 to 33 times less than in the other species. It is interesting that, with respect to the number of individuals in which PGCs with nuclei in a polymorphous state were found (table 16), the Atlantic salmon occupies a diametrically opposite position to that of the pink salmon.

In describing the development of the gonads in diadromous salmon, special attention has been directed to determining the times of onset of the individual stages. Selected for purposes of comparison were the periods in which PGC concentration occurred, the oocytes of the synaptic stage appeared, and protoplasmic growth of the oocytes began. Apparently, the period of PGC concentration begins at almost identical times - with the number of degree-days comprising 15-20% of the number of degree-days for the entire period of incubation (table 17). The somewhat higher percentage in the sockeye, masu and coho is possibly due to the absence of earlier material for these species. The rate of development from the oogonium to the oocytes of the synaptic stage, essentially prior to the completion of sex differentiation, varies in its intensity. It is highest in the pink salmon, in which the oocytes of the synaptic stage appear at the beginning of the final third of the incubation period, i.e., even in the embryos, which (calculated as a percentage of degree-days) is 1.5 to 2.5 times more rapid than is the case with the other salmonids (table 17).

Also deserving of attention is the dissimilar state of the gonads at the time of hatching. Whereas in pink salmon, well-formed ovaries with oocytes in the synaptic, pachytene and diplotene stages are already present at this time, in the remaining species it is either only the

gonia (chum), or alternatively, the gonia and the as yet primordial germ cells during the period of mitotic division (coho), or yet again, as is observed in Atlantic salmon, only the PGCs even before the beginning of mitotic division (table 18) that are present.

Table 16 68

Frequency of occurrence of primordial germ cells with dissimilarly shaped nuclei during the period when mitotic PGCs begin to appear in diadromous salmon

1 Вид	2 Исследовано рыб			3 Проверено ППК					
	4 всего экз.	5 из них имели ППК с полиморфными ядрами		7 всего ППК	8 из них имели ядра, %				
		6 экз.	%		9 округлые	10 полиморфные	11 овальные	12 в митотическом состоянии	13 всего
Горбуша 14.	33	14	42,4	1879	83,4	2,4	9,4	3,4	98,6*
Кета 15.	21	14	66,6	451	75,8	10,4	13,8	0	100
Сима 16.	6	6	100,0	121	18,3	68,3	13,4	0	100
Нерка 17.	7	7	100,0	284	48,4	50,6	0	1,0	100
Кижуч 18.	11	10	91,0	361	65,7	28,0	4,4	1,9	100
Атлантический лосось (семга) 19	34	32	94,1	1896	20,6	78,7	0	0,7	100

20 * Кроме того, у 1,4% клеток ядра имели форму переходную от полиморфной к овальной.

Key: 1. Species. 2. Fishes examined. 3. PGCs verified. 4. Total number of specimens. 5. Those which had PGCs with polymorphous nuclei. 6. Specimen. 7. Total of PGCs. 8. Those which had nuclei, %. 9. Spherical. 10. Polymorphous. 11. Oval. 12. In a mitotic state. 13. Total. 14. Pink. 15. Chum. 16. Masu. 17. Sockeye. 18. Coho. 19. Atlantic salmon. 20. Moreover, in 1.4% of the cells, the nuclei were transitional in shape, between polymorphous and oval.

Table 17

Times of commencement of some stages of gametogenesis in juvenile salmon of the genera Oncorhynchus and Salmo

1 Вид	2 Номер и характеристика этапа (по схеме № 5)			7 Колич. градусо-дней за весь период инкубации (в данной партии)
	3	9	10	
	3 концентрация ППК в области будущей закладки гонад	4 появление ооцитов		
		5 синаптической стадии	начала протоплазматического роста 6 (1-я ступень)	
Горбуша 8	90(15,0)	415(69,3)	650(108,6)	598
Кета . 9	86(22)	640(>163)	1394(222,6)	626
Нерка . 10	292(44)	728(>110)	961(146,4)	660
Сима . 11	200(37,7)	889(166,7)	1134(212,7)	530
Кижуч . 12	128(39,7)	834(259)	1393(432)	320
Семга . 13	70(19,4)	973(>229)	1048(291)	360

14 Примечание. Цифры без скобок — колич. градусо-дней к началу этапа гаметогенеза в абсолютных цифрах; в скобках — в процентах к колич. градусо-дней за весь период инкубации.

Key: 1. Species. 2. Number and description of stage (according to scheme No. 5). 3. Concentration of PGCs in the region of future gonadal establishment. 4. Appearance of oocytes. 5. Of the synaptic stage. 6. Of the beginning of protoplasmic growth (1st phase). 7. Number of degree-days over the entire period of incubation (in the given batch). 8. Pink. 9. Chum. 10. Sockeye. 11. Masu. 12. Coho. 13. Atlantic salmon. 14. Note. The numerals without brackets denote the number of degree-days by the beginning of gametogenesis, in absolute figures; in brackets - percentages of the number of degree-days over the entire period of incubation.

Table 18

69

Characteristics of the germ cells in diadromous salmon larvae of the genera Salmo and Oncorhynchus during the hatching season

1 Вид	2 ППК		7 Гонии последующих порядков 5	Ооциты синаптической стадии и диплотены 6
	с полиморфными ядрами 3	в митотическом состоянии 4		
Семга 7	+			
Кижуч 8	+	+		
Нерка 9		+	+	
Кета 10			+	
Горбуша 11			+	+

Key: 1. Species. 2. PGCs. 3. With polymorphous nuclei. 4. In the mitotic state. 5. Gonia of successive orders. 6. Oocytes of the synaptic and diploneme stages. 7. Atlantic salmon. 8. Coho. 9. Sockeye. 10. Chum. 11. Pink.

At the time when female far eastern salmon are migrating to the sea, the condition of their oocytes may differ markedly due to peculiarities in their biology. In pink salmon, gonadal development begins early and progresses rapidly. In the remaining far eastern salmons a slower rate of development of the gonads is observed and individual differences in the times when sexual maturation occurs may be as much as several years. Moreover, the sockeye salmon includes freshwater forms, which may well account for the peculiarities of its gametogenesis. To some extent this explanation also holds true for the coho, of which there is no proof of the existence of freshwater forms, even though immature fishes may remain in the river for protracted periods. In the Atlantic salmon, during the initial period of life in the sea a rapid rate of growth is to be expected. Apparently, the earlier condition of the oocytes at the time when juvenile Atlantic salmon are migrating to the sea is highly advantageous in the realisation of this process.

It should be noted that when juvenile salmon are making the transition to living in the sea, at first, growth through "fattening" must be relatively more rapid. Accordingly, an immediate transition of the oocytes to trophoplasmic growth can hardly be expected. Here, the existence of some kind of "transitional" period must of necessity be assumed.

In the males of all salmonids, except for the "dwarf" forms, the state of the testes during the period of catadromous migration is identical (Scheme 5). Only spermatogonia are found in the testes and there is a gradual increase in their numbers. The beginning of active spermatogenesis occurs in the sea shortly before the spawning run or (in the case of an early migration - the autumn salmon), later still, upon entering the river for spawning or even after that. 70

Pre-gonadal stage:

1. Individuation of PGCs.
2. Migration of PGCs.
3. Concentration of PGCs in the region of gonadal establishment.

Emergence of gonads:

4. Formation of genital ridges.
5. Polymorphous state of the nuclei of PGCs.
6. Mitotic division of PGCs.
7. Mitotic division of the gonia and somatic cells of the gonad.

Sex differentiation:

8. Anatomical and cytological differentiation.
9. Oocytes of the synaptic and diplotene stages.
10. Oocytes of the beginning of protoplasmic growth - 1st phase.
11. Concentration of RNA in the cytoplasm in the perinuclear region - 2nd phase.
12. The same, at the periphery of the oocytes - 3rd phase.
13. Emergence of the yolk nucleus - 4th phase.
14. Vacuolation of the cytoplasm - 5th phase of the period of protoplasmic growth of the oocytes.

9. Spermatogonia.
10. Anatomical emergence of the testes. Mitotic division of the spermatogonia.

Migration to the sea.

Scheme 5. Stages of the early period of gametogenesis and gonadal development in diadromous salmon (prior to the transition to the sea mode of life).

Note: Sex differentiation in pink salmon males occurs differently from the manner indicated in this scheme (p.61).*

Degree of development of the ovaries in juveniles in the course of catadromous migration

Although in diadromous salmon, during the period of catadromous migration the oocytes are in a state of protoplasmic growth**, the time frames and distinctness of this process differ in them. Depending on the moment when the nucleic acids become locally concentrated the period of protoplasmic growth 71 of the oocytes in diadromous salmon can be divided into several arbitrary phases.

In describing the state of the oocytes in each of the phases it is necessary to preface this with several remarks that are common to all of the diadromous salmons. They apply primarily to the exponents of the sizes of the nuclei and oocytes during the period of protoplasmic growth. For these purposes a study was made of salmonid parrs and smolts aged between three and 30 months, which had been caught in river mouths and in certain areas of the Baltic Sea.

The largest oocytes and nuclei with diameters of up to 240 and 108 microns respectively were found in females aged 1 + years, caught on August 5, 1956 in the Salatsa River. Consequently, after the female had been in the river for more than 18 months the diameter of the oocytes, if calculated from the diameter of the PGCs (24–30 microns), had increased

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*Of original text (Tr.).

**It would probably have been more correct to use the term "cytoplasmic growth", however, in the ichthyological literature the term "protoplasmic growth" has been adopted.

approximately tenfold. At the same time it is known that the definitive dimensions of the eggs of Baltic salmon are about 5 mm. Consequently, during the sea period of its life the diameter of the oocytes of a Baltic salmon increases approximately 20-fold (table 19). This is characteristic of a higher degree of intensity of oocyte growth during the sea period of life than during the river period in first maturing individuals.

Table 19

Degree of intensity of oocyte growth in Baltic salmon females during the river and sea period of life

1 Период	2 Вес рыбы, г	3 Длина рыбы, мм	4 Диаметр половых клеток, мм
5 Вылупление	0,1	17	0,025
6 Миграция молоди из реки в море	5	150	0,24
7 Нерест	10 000	900	5

8 Примечание. Все цифры даны округленно; данные для первой и второй граф составлены по материалам настоящей работы; показатели третьей графы составлены по литературным данным (Берг, 1949; Баранникова, 1962).

Key: 1. Period. 2. Weight of fish, g. 3. Length of fish, mm. 4. Diameter of germ cells, mm. 5. Hatching. 6. Migration of the young from the river to the sea. 7. Spawning. 8. Note. All of the digits are rounded. The data in the first and second columns are compiled from information contained in the present work. The indices in the third column were compiled from published data (Berg, 1949; Barannikova, 1962).

Interesting data are obtained when comparing the volumes of the nucleus and the oocyte. At first, the growth of the volume of the nucleus predominates over the growth of the volume of the oocyte. Therefore, the observed increase in cell dimensions is occurring chiefly on account of

the increase in volume of the nucleus. This situation is well illustrated by data on the ratios of the diameter of the nucleus to the diameter of the cell. In 85 to 326 day-old females this index exceeds 50%. Only in 72
fishes aged between 1 + and 2 + does it decrease slightly and become less than 50%. This affords a basis for assuming that the growth of the oocytes is at the expense of a build-up of the mass of cytoplasm, i.e., truly protoplasmic growth begins to be clearly manifested in young Baltic salmon females only a short time prior to their migration to the sea.

A detailed description of the oocytes of the protoplasmic growth period is given with special reference to salmonids. Isolated in the study were five states of the oocytes, which are called the phases of oocyte development of the protoplasmic growth period (Persov, 1966c). The first phase characterises the beginning of protoplasmic growth of the oocytes, when several parietally arranged nucleoli become clearly visible in their nuclei (plate XIII, 1). By this time the diameter of the nuclei has increased to 18-20 microns, the boundaries of the oocytes have become distinct and there is a well-defined layer of pale cytoplasm.

In pink salmon the first phase begins at 650 degree-days, which, for the incubation period in the batch in question, is 108.6% with respect to the number of degree-days. In chum, the first phase begins at 1394 degree-days (222.6%), in sockeye - at 961 degree-days (146.4%), in masu - at 1134 degree-days (212.7%), and in coho - at 1393 degree-days (432%). Of course, these indices are largely dependent on the conditions of incubation, foremost among which is the temperature. Nevertheless, they provide a rough index of the extent of the differences between the times when protoplasmic growth of the oocytes begins in representatives of the various species of diadromous salmon.

The second phase of development of the oocyte/protoplasmic growth period is characterised by localisation of RNA in the cytoplasm in the perinuclear zone. In young oocytes of the post-synaptic period the cytoplasm is still homogeneously pigmented. Gradually, certain of its zones take on a brighter pigmentation (lacquer). The changes in the arrangement of these zones, the number of them and their interrelation have a definite order of succession. These patterns are evidently a reflection of functional changes occurring in the oocytes during the given period.

Initially, close to the nuclei of the oocytes several more darkly pigmented, individuated, cytoplasmic zones are to be seen (plate XIII, 2-3). The chromosomes in such cells are clearly visible and are in the form of typical "lamp brushes" (plate XIII, 3). Similar patterns begin to be found in oocytes that have attained a certain size, with the diameter of the nuclei not less than 30 microns (it is more convenient to judge the sizes of the oocytes from the diameter of the nuclei, since the cells are often shaped in such a way that it is difficult to obtain an exact measurement of their diameter). Gradually there is an increase in the number of brightly pigmented cytoplasmic zones. They now occupy a larger part of the oocyte and may sometimes be in the shape of a "half-moon".

The zones of cytoplasm, intensely sensitive to hematoxylin lacquer, 73
are also stained by gallocyanin (plate XIII, 4) and azure-eosin according to Romanovskii. Upon extraction of the nucleic acids by treatment of thin sections with hydrochloric or trichloroacetic acid (Pirs, 1962) they remain achromatic. This makes it possible to assume that in cytoplasmic zones selectively stained with gallocyanin (Nucleic Acids, 1957) and azure-eosin (Roskin and Levinson, 1957), RNA concentration is occurring. In the

various species of diadromous salmon this process begins at different times, although in the pink salmon it begins much earlier than in the remaining representatives of the genera Salmo and Oncorhynchus (table 20). In specimens fixed in osmic acid, according to the Kolachev-Nasonov method, fat droplets are visible in the cytoplasm of the oocytes. They do not have a regular pattern, although more often they can be found in the perinuclear zone.

It is in the third-phase of oocyte development that the patterns of RNA localisation in the cytoplasm along the periphery of the oocytes are most exponential (plate XIV, 1,2,3). This zone will be denoted by the term "peripheral ring". The cytoplasm around the nucleus is much more faintly stained with ferric hematoxylin, according to the Heidenhain method, and with gallocyanin (plate XIV, 4) than is the remaining part. It therefore appears brighter. In the individual zones of the "peripheral ring", single large, fat droplets are visible (plate XIV, 5), as well as some larger groupings of 5-6 droplets.

Table 20

Times of commencement of the individual phases of development of oocytes in the protoplasmic growth period (age in months of hatching)

1 Вид	2 Ступени				
9	1-я	2-я	3-я	4-я	5-я
3 Горбуша	0,5 - 1	1—2	1—2	5—6	5—6
4 Кета	3	4	6	7—8	—
5 Нерка	3—4	4	7	15—16	17—19
6 Сима	2—3	5—6	—	—	—
7 Кижуч	2—3	5—6	6—7	12	—
8 Семга	3—4	4—5	12—24	—	—

Key:
1. Species
2. Phases
3. Pink salmon
4. Chum
5. Sockeye
6. Masu
7. Coho
8. Atlantic salmon
9. 1st.

The commencement times of the third phase differ especially in the pink salmon and the Atlantic salmon: from one to two months and one to two years respectively (table 20). In four Atlantic salmon females at age 2+ years, during the period of their migration from river to sea (Umba River, 1965), 361,068 germ cells were tested. Of this number, 11.4% were oogonia, 56.6% were synaptic stage oocytes, 10.9% were oocytes in the pachytene and diplotene stages, and 1.6%, 1.8% and 11.5% were oocytes of the first, second and third phases of the protoplasmic growth period*. 74

The ovaries of young pink salmon females migrating to the sea are in the same state as those of young Atlantic salmon, even though the river period of life of the former is much shorter. The oocytes may remain in the third phase of development for a protracted period, e.g., 8-9 months in the sockeye (table 20).

Subsequently, the "peripheral ring" disappears and the cytoplasm is again homogeneously pigmented. Now, the formation known as the yolk body is clearly visible in it (plate XV, 1,2). This state of the oocytes may be defined as the fourth phase of development during the protoplasmic growth period.

The yolk bodies are more often discerned at the periphery of the oocytes.** Usually, it is as if they have a double contour - an outer zone, demarcating the zone of their positioning, and an inner zone. The sizes of the yolk bodies may range from 10 to 20 microns, and those of their zone of positioning - from 20 to 40 microns. Often seen at the centre of a yolk formation are minute vacuoli. These stand out particularly well when there is staining with gallocyanin with a naphthalene-yellow finish.

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*All these data on the composition of the germ cells in four Atlantic salmon females were taken from a paper written for a diploma by L.A. Ivanchenko (1966) and prepared under my supervision.

**This is by no means indicative of their being formed here. On the contrary, there are grounds for believing that their formation occurs in the perinuclear zone.

Oocytes of the fifth phase, when vacuoli are appearing in the cytoplasm, are seen in only two of the species - pink salmon and sockeye, inasmuch as it has not proved possible to rear chum and coho for longer than 8 and 12 months. Masu were not reared at all, and Atlantic salmon females migrate with the oocytes to the sea no later than the third phase of the protoplasmic growth period.

At a certain stage of oogenesis the yolk bodies disappear and vacuoli are seen. Initially these occur only along the periphery, but soon afterwards they can be found in any region of the oocytic cytoplasm (plate XV, 3,4). Subsequent to osmic acid fixation, large fat droplets are clearly visible along the periphery of the occytes among the vacuoli (plate XV, 6). Besides the large fat droplets, a considerable number of small ones are seen; these border the individual vacuoli and are also distributed in the immediate proximity of the nucleus.

The question as to the nature of the formations being discerned in the cytoplasm of the oocytes in the various phases of the protoplasmic growth period* is still under discussion. Diadromous salmonids have been 75
shown to have a specific stainability with gallocyanin and azure-eosin. This gave grounds for interpreting the dark regions of cytoplasm as sites of RNA concentration. One view is that there is a link between such formations and the Golgi network (Mendoza, 1954). Some of the divergent opinions in evaluating them may be due to differences in terminology, for example, "peripheral ring" (in the present work) and "vitelline ring" (Lams, 1903-1904).

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*The patterns pertaining to the differing state of the oocytes during the protoplasmic growth period which were described for the Sevan trout (Negonovskaya, 1966) are closely similar to those being treated in the present work as phases of development.

Deserving of special study is the question of the similarity between the patterns found for the Osmeridae and the Salmonidae, with "circumnuclear rings"* in the oocytes of the mirror carp (Gerbil'skii, 1939), ludoga whitefish (Lapitskii, 1949), carps and carp X eastern carp hybrids (Kuz'min, 1957).

The detailed description of the state of the oocytes, with respect to the separate phases of the protoplasmic growth period, may be of practical importance. For example, for Baltic cod it was demonstrated that "in sexually mature females the oocytes of this period attain phases 4b and 4c, whereas in sexually immature females they are only in developmental phase 4a" (Shirokova, 1971). The same author showed that the possibility of segregating sexually mature and immature females by a character such as this has a potential application in short-term predictions of commercial catches of Baltic cod.

The study of the structure of the cytoplasm in the course of protoplasmic growth of the oocytes should also prove useful from the standpoint of obtaining a more profound understanding of the yolk formation process. Already in one of the first investigations of the ultrastructure of the circumnuclear zone of young oocytes of certain teleosts an intimate association between the nucleus and the cytoplasm has been revealed, the possibility of a metabolism has been indicated and the contraction of the circumnuclear zone during yolk formation has been traced (Porte and Zahnde, 1962). More recently, DNA has been discovered in the cytoplasm of the oocytes, the quantity of which is thousands of times greater than in the nucleus (Zbarskii,

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*It seems that the differences between them are greater than the similarities, since "peripheral rings" are associated with age and the state of the oocytes, while "circumnuclear rings" are described as a seasonal phenomenon.

1966). The formation of strong groupings of DNA with other polymers, particularly with RNA and albumen, has been demonstrated. In a specially conducted study of frog and sturgeon oocytes, the presence of DNA in the cytoplasm of the oocytes of only the early stages of development has been ascertained (Shmerling, 1966). In the view of this latter author "the impression is created that in this stage of oogenesis the synthesis of nucleic acids takes place mainly in the cytoplasm" (p.346). Although an active exchange of proteins and nucleic acids in the cytoplasm can also take place in the absence of a nucleus, the appearance of DNA nevertheless 76
has its origins in an excessive production of them in the nucleus (Shmerling, 1966). In discussing the nuclear-cytoplasmic ratios in the course of development of the oocytes the suggestion is made that "it is probable that the nucleus is not only a supplier of information molecules but is also under the influence of information coming to it from the cytoplasm" (Zbarskii, 1966, p.325).

From this point of view, data on the localisation of nucleic acids in the cytoplasm of the oocytes during the protoplasmic growth period can provide evidence of an intensive metabolism and of a changing nuclear-cytoplasmic ratio during development of the oocytes. Undoubtedly, this question deserves to be the subject of a special comparative study.

Sex ratios in the young

In essence, the problem of sex breaks down into three independent problems: sex determination, sex differentiation and the ratio between the sexes. Fundamental to the first problem is the question of when sex determination occurs, i.e., does it take place prior to fertilisation (progamically), at the moment of fertilisation (syngamically) or after

fertilisation (epigamically)? The second problem includes a number of questions: what is the mechanism of the sex differentiation process, when does it begin, and on the basis of which anatomical characters would it be possible, long before the appearance of oocytes and spermatocytes, to form a judgment as to the direction of sex differentiation? The third problem is linked with solving the question of the ratio between the sexes in the various stages of existence of a population.*

In fishes, for example, besides the primary sex ratio, which is established during the sex determination period, and the secondary, which reflects the ratio between the sexes during the hatching period, a tertiary sex ratio should also be characterised, the indices of which may vary in the course of the life of a population or species. According to these questions the first problem is primarily genetic, the second - embryological, and the third - ecological.

As is well known, the ratio between the sexes is one of the factors characterising population fecundity. A predominance of females, all other conditions being equal, is one of the ways of preserving and increasing the numbers of a given species. The development of this theme is of practical importance, for example, in the far eastern salmon fisheries, where the breeding of salmon takes place under markedly different conditions (water temperature, duration of incubation, keeping of the larvae, fattening of the young, length of the migration routes), which may have an effect on the ratio between
/ numbers of young males and females during the river-to-sea migration period. Such a study is also of interest from the standpoint of resolving another 77 question: whether a relationship exists between the numerical sex ratios

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*For establishing the numbers of males and females during the next recruitment of commercial stocks, it is possible that reverse information concerning the number of males in the population will be of great importance (Geodakyan, 1965,1969; Fishelson, 1970).

in migrating young and in brood stock entering particular rivers. This, in turn, would enable additional facts to be ascertained for the purpose of arriving at a more precise definition of the biological phenomenon currently judged to be a "homing instinct". Furthermore, information on the ratio between the sexes is of importance in a comparative characterisation of young reared in artificial hatcheries and those spawned under natural conditions. Ultimately, the accumulation of factual data on the ratio between the sexes of juveniles and brood stock of the far eastern salmon fisheries should lead to the organization of a more soundly based biotechnology for use in the artificial rearing of far eastern salmonids.

Despite the existence of a large body of data on the subject of sex ratios in adult ichthyoids and fishes, there is only a limited amount of such information on the young of those organisms. In some studies, comparative data are presented for both young and mature individuals. Thus, in British Columbia in 1930, in sockeye salmon migrating to the sea there were 142 males for every 100 females, and in the brood stock that had arrived for spawning in that year, males outnumbered females to the extent of 168 per hundred (Foerster, 1954). In young lampreys, females predominated; in the brood stock - males (Hardisty, 1960). Some information on sexually immature diadromous fishes of commercial value is presented in a work by Yandovskaya (1941). Just how wide the range of indices of the sex ratios in fishes is can be seen from the data in table 21. The variations are not only substantial in the different species. They are also large within one and the same species in the different areas of the geographic range and in different years. Pertinent published data exist for pink salmon (Soldatov, 1912; Pravdin, 1928; Semko, 1939), chum (Soldatov,

1912, Kuznetsov, 1928), masu (Krykhtin and Smirnov, 1962) and sockeye (Kuznetsov, 1928).

The scantiness, and at times even the absence of such information with respect to young fishes, for example, those that are diadromous during the seaward migration period, is primarily on account of the fact that it is far from an easy matter to determine the sex to which a fish belongs. For a clear understanding of the normal course of development of the gonads, a special study of the question of sex differentiation indices for a given species is required. As exemplified by such subjects as the pink salmon, loach and vimba, it can be seen that this problem is not so simple after all.

Inasmuch as it was in pink salmon fingerlings (O. gorbuscha) that the development of the gonads was traced in greatest detail, this was the species selected as the subject for a study of sex ratios in the young. The fry were obtained from fish-rearing stations and also directly from the rivers of Southern Sakhalin, the Kuriles and the Arctic. Observations relating to the Southern Sakhalin hatcheries were performed over a three-year period. Those relating to the arctic hatcheries and the rivers of 78
Southern Sakhalin spanned a two-year period. In all, 10,575 O. gorbuscha specimens were studied.

By the time of migration from river to sea, in young pink salmon and chum the gonadal differentiation process is usually already complete. In males in this stage of ontogeny the testes are in the form of very fine, almost transparent threads, which cover the entire length of the swim bladder. In histological specimens, it is only germ cells of the earliest stage of development - spermatogonia -, that are detected in such testes.

The more solid ovaries are also arranged on both sides of the swim bladder, although only along its anterior half. They are therefore much shorter than the testes. Even with the naked eye it is often possible to make out the tuberosity on the surface of the ovaries, which is due to the presence of the already large oocytes.

Thus, in young pink salmon and chum, during the migration season the sex of the females can be visually determined through the use of a certain amount of skill. All the same, in a number of instances it proved necessary to prepare histological specimens. An especially large number of these were made for the purpose of sexing the pink salmon fry from Reidovoi hatchery, since a heavy predominance of males was observed there in the course of an external survey (table 22). The visual findings were 79
confirmed by the results of histological analysis. To provide for an additional check, material from one and the same sample was examined by several co-workers. Here too, there proved to be a coincidence of the data derived by different investigators. Finally, the same material was checked visually and was later rechecked using the histological specimens. The discrepancy amounted to 5.5 - 8.6%. Thus, the control checks that were performed confirmed the objectivity of the indices on sex ratios in fingerlings, derived through visual examination. Nevertheless, despite the relatively small percentage of errors, this procedure is in need of refinement.

Table 21

Sex ratios of some sexually mature fishes*

78

Species	Number of males per 100 females
Coregonus nobilis	687
C. coerulenus	529
C. alpinus	407
Salmo fario	391
S. salar	181
Amiurus nebulosus	140
Clupea harengus	100
Pleuronectes platessa	100
Gadus morhua	75
Hippoglossus hippoglossus	66
Gadus aeglefinus	53
Merlanus merlanus	47
Limanda limanda	33
Carassius auratus	13
Gambusia holbrooki	12
Misgurnus fossilis	11

*From Traité Zoologie, Paris, Vol 13, p.1608

Table 22

Sex ratios (visually estimated) in pink salmon fingerlings measuring 34 mm and more in length at the time of their release from hatcheries on the southern part of Sakhalin Island

79

1. Завод	1961 г.		1962 г.		1963 г.	
	2. всего, экз.	3. колич. ♂♂ на 100 ♀♀	2. всего, экз.	3. колич. ♂♂ на 100 ♀♀	2. всего, экз.	3. колич. ♂♂ на 100 ♀♀
4. Активный			472	114,8		
5. Анивский			435	78,2	213	126,5
6. Березняковский			382	100,0		
7. Ватутинский			177	96,6		
8. Кирилловский					189	121,7
9. Краснопольский			222	79,0		
10. Курильский			398	89,9		
11. Лесной					258	145,7
12. Ловецкий			477	72,2		
13. Осенний			455	123,0		
14. Парусный			390	74,9		
15. Поронайский			198	127,7	163	53,7

16. Пугачевский			189	89,0	132	164,0
17 Рейдовый			296	212,0		
18. Соколовский	346	111	393	75,9	869	109,4
19. Сопочный			385	84,1		
20. Таранайский			505	92,8	179	94,5
21 Урожайный					399	133,3
	346	111	5434	95,0	2402	115,2

Key: 1. Hatchery. 2. Total number of specimens. 3 Number of males per 100 females. 4. Aktivnyi. 5. Aniva. 6. Bereznyaki. 7. Vatutino. 8. Kirillovo. 9. Krasnopol'e. 10. Kuril'skii. 11 Lesnoi. 12. Lovetskoe. 13. Osennii 14 Parusnoe 15. Poronaiskii. 16. Pugachevskii. 17. Reidovo. 18 Sokolovka. 19. Sopochnyi. 20. Taranai. 21 Urozhainoe.

CHAPTER 4. THE FORMATION OF INDIVIDUAL FECUNDITY DURING THE PERIOD OF EARLY GAMETOGENESIS

The question of the factors regulating the individual fecundity 80
of fishes has not received sufficiently detailed treatment in the literature (Nokol'skii, 1965). Meanwhile, fluctuations in absolute fecundity are only possible when based on a change in the stock of reserve germ cells. This in its turn is dictated by the specifics of development of the gonads. As regards the role of external and internal factors, it is safe to say that a change in the conditions of the environment is what actuates the mechanism regulating the fecundity of fishes.

In this section of the book an attempt is made to analyse the mechnaism regulating the fecundity of pink salmon. Over and above its own biological properties (monocyclicity, early sexual maturation and short life cycle), this is of interest as the subject of a widely staged experiment on acclimatisation conducted in the basins of the Barents and White seas. Eggs in the eye pigmentation stage (incubation two-thirds complete) are delivered from Southern Sakhalin. The final third of the

incubation, and the holding and fattening of the fry, right up to the time of their migration to the sea, occurs in the arctic hatcheries. In this way, the life cycle of an acclimatised pink salmon begins on Southern Sakhalin and ends in the Far North. Consequently, the essence of the "experiment" in the case being discussed consists in the fact that one part of the pink salmon eggs from the same spawning remains in fresh water conditions, while the other part becomes subject to the conditions of the new geographic range.

The brood stock that had arrived to spawn in the arctic rivers in 1960 and 1961, that is, in the first years at the outset of the acclimatisation studies, were characterised by larger dimensions and greater fecundity, although the weight of the ovaries and especially of the eggs contained in them proved to be substantially less than in the case of the pink salmon that had entered the Southern Sakhalin rivers to spawn (table 23). It is important to note that in both regions (Southern Sakhalin and the Arctic) an enhancement of fecundity correlates with an increase in the sizes of the brood stock. On Southern Sakhalin, however, in large pink salmon there is not only an increase in absolute fecundity, but also in the weight of the ovary and the individual eggs, whereas in the Arctic, the rise in the fecundity of the pink salmon is paralleled by a decrease in the weight of the individual eggs.

Consequently, in the process of a pink salmon adapting to the new range, two interesting facts associated with the dynamics of its fecundity were manifested: there was an increase in absolute fecundity and a decrease in the weight of the eggs and the ovaries (table 23).

Table 23

Comparative indices of pink salmon brood stock

1 Показатель	2 Южный Сахалин (1957—1960 гг.)		3 Заполярье			
			1960 г.		1961 г.	
4	длина ♀, см		длина ♀, см		длина ♀, см	
	45—49	50—54	45—49	50—54	45—49	50—54
5 Абсолютная плодовитость, количество икринок . .	1432	1567	1797	1950	1642	1890
6 Вес:						
7 самки, г	1090	1475	1290	1548	1213	1500
8 яичников, г	192	233	149	193	116	147
9 одной икринки, мг . .	134	149	83	99	71	80

Key: 1. Index. 2. Southern Sakhalin (1957-1960). 3. Arctic. 4. Length of female, cm 5. Absolute fecundity, number of eggs. 6. Weight 7. Of a female, g 8 Of the ovaries, g. 9 Of a single egg, mg.

81

In order to determine the dependence of the fluctuations in the individual fecundity of pink salmon on the original stock of germ cells, a comparison was made between their numbers in the gonads of young and sexually mature females. In the latter, at the time of entering the rivers there are only oocytes of a definitive condition (oogonia and oocytes of earlier stages were not discovered in these gonads), and the number of them can be determined visually. For calculating the number of germ cells in fingerlings, special procedures must be used.

In comparison with other salmonids, gonadal development in pink salmon, as already mentioned, takes place very rapidly and there is an appreciable displacement into the embryonic period. Between 18 and 20 days after fertilisation (at this point and at all times hereinafter the dates indicated are for incubation at a temperature of 9-10°) PGCs are discovered

These soon begin to divide. By the 35th to the 39th day after fertilisation PGCs are no longer in evidence and mass mitoses of gonia of subsequent orders are seen in the gonads. Subsequently, oocytes of the synaptic stage of development appear, and prior to hatching it is the oocytes of the early diplotene stage that predominate. Several days after hatching, a substantial number of the oocytes are already in the protoplasmic growth stage. By the time the pink salmon fry migrate from the river to the sea this is nearing completion.

In the course of studying the process of gonadal development it was found that, due to mitotic reproduction of PGCs (originally between 29 and 50 of them were discovered), by the time of hatching more than 3,000 germ cells are manifested. Thereafter, the number of them increases, reaching a peak in the months of March and April in the North, and evidently, from one to one and a half months earlier on Southern Sakhalin After this it begins to fall and by the time the fingerlings migrate it has decreased by a factor of two to 2.5.

According to published data (Dvinin, 1959; Chernyavskaya and Tankov, 1959), the fecundity of pink salmon at the time of entering the rivers of Southern Sakhalin amounts to approximately 1,600 eggs. According to records compiled by the Sokolovka fish hatchery for the years 1958 and 1960 there are 1,545 eggs. Our data, derived from an itemised count of all of the eggs and pertaining to Southern Sakhalin in 1960, show that the individual fecundity of the 9 females studied ranged from 1,089 to 2,030, the average count being 1,425 eggs. Regardless of which of these indices is utilised, it remains evident that the number of oocytes in pink salmon fry at the time of their seaward migration is

82

greater than the number of them in females entering the rivers to spawn. Consequently, it must be assumed that in the sea, the number of germ cells diminishes as a result of a certain proportion of them dying off. Indeed, in the study of the histological specimens, oocytes in a state of degeneration were discovered. Somewhat similar patterns were noted in the ovaries of the young females even prior to the beginning of migration Apparently, it is as a result of this process, which begins in the river and continues in the sea (Grachev, 1968, 1971), that the number of germ cells falls to the level of the individual fecundity typical of a sexually mature pink salmon. Under the conditions obtaining in northern waters, degeneration proceeds less rapidly. This is confirmed by the quantity of dying "superfluous" oocytes. In the sea off Southern Sakhalin, an average of 290 oocytes perish in a single individual (as compared to 1,890 in alevins at the time of migration, and 1,600 in the brood stock), which is 15.3%. The corresponding figures for the Arctic (1960) are 258 oocytes (2,108 in the fry and 1,850* in the brood stock), or 12.2%. Accordingly, an expansion or contraction of the oocyte degeneration process in pink salmon is one of the mechanisms by which fluctuations in fecundity are produced. In the case being discussed, degeneration of the oocytes is of major importance from the standpoint of adaptation.

The reasons for the decrease in the sizes of the eggs of the pink salmon in its new range continue to be only partly understood. At the same time, as has been demonstrated (Rass, 1947), under certain conditions this index becomes important taxonomically. It is conceivable that the reduction in egg sizes is due to a shortening of the trophoplasmic growth

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*Based on data supplied by V.V. Azbelev and G.D. Gromov (1960).

period, since the migration of the fry in the Arctic begins from one to one and a half months later than it does on Southern Sakhalin, and the brood stock enter the rivers for spawning on almost the same calendar dates. If this hypothesis is true, it means that by altering the biotechnology used to obtain the roe and by changing the incubation and rearing conditions, an earlier release of the fry could be achieved. Under these conditions the foraging season of pink salmon in the Arctic will accordingly be prolonged, that is, conditions will be created for a lengthening of the trophoplasmic growth period, which will ultimately lead to an increase in the sizes of the eggs.

The bioengineering aspect of the problem, namely the possibility 83
of obtaining pink salmon larvae capable of migrating at an earlier date, was demonstrated by the results of studies conducted in 1961-1962. In August 1961, a pink salmon roe was obtained at the Umba fish hatchery by the hypophysial injection method. It was then delivered to the laboratory where the eggs were preincubated and the larvae maintained at temperatures of between 4.5 and 17° (at the Umba hatchery the temperature at the beginning of incubation was 13.7-16.7°). From the larvae of this batch of eggs, it proved possible by February 10, 1962, to grow a pink salmon under laboratory conditions which had a weight of up to 1,480 mg and a length of 60 mm. Consequently, long before the beginning of migration, which takes place in May on Southern Sakhalin and in July in the Arctic (Il'ina, 1960), a juvenile fish was obtained, the weight of which exceeded by several times that of pink salmon fingerlings at the time of their release from the hatcheries (ordinarily such a fingerling weighs about 300 mg).

In the opinion of many investigators, larger females are more fecund and produce a larger egg. Nevertheless, the findings adduced in the present work show that, when there is an abrupt change in the conditions, such as, for example, the acclimatisation of the far eastern pink salmon in the basins of the White Sea and the Barents Sea, an increase in its dimensions and fecundity may be accompanied by a decrease rather than an increase in the sizes of the eggs. The possibility of there being unlike variants of the correlation between absolute fecundity and egg sizes is also confirmed by data contained in the literature (Lyamin, 1956; Zotin, 1961).

In ichthyology, the problem of fecundity in females is usually considered from the standpoint of three different aspects: individual, species and population fecundity.* Individual fecundity means the number of eggs laid by a female during a single spawning season, species fecundity means the number laid during her entire life, and population fecundity means the number of eggs laid by all the females of a given population under the actual conditions obtaining in a given region, at a given sex ratio and a given age structure.

In the classification just presented the main index is the end product of the gonadal functions, namely, the fecundity actually being observed. It is evidently because of this that the question of the potentials for a change in fecundity and of the mechanisms producing fluctuations in it has been inadequately covered in the literature**.

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*A detailed account of the notions pertaining to fecundity can be found in a monograph devoted to this problem (Anokhina, 1969).

**In the monographic survey "Patterns of change in the fecundity of fishes" (Anokhina, 1969), this problem also, regretfully, has not been accorded due consideration.

For example, in comparing the fecundity of pink salmon in the parental far eastern waters and under the acclimatisation conditions in the North, 84
it turns out that individual fecundity is capable of increasing by not more than 15 to 20%. At the same time, if we compare the number of oogonia and oocytes with which pink salmon begin the meiotic cycle, the differences become more substantial.

In the ontogeny of pink salmon it is possible to distinguish two indices of fecundity: "potential" and "ultimate" (Persov, 1963b), and it is the relation between these which will be the main determinant of the individual, species and population fecundities. As applied to monocyclic species, it is correct to maintain that potential fecundity must be considered from two aspects: true fecundity, which is established immediately after sex differentiation, and initial fecundity, which characterises the number of oocytes that have completed protoplasmic growth and are ready to make the transition to trophoplasmic growth (Kuznetsov and Kukharenko, 1971).

In contrast to the monocyclic and polycyclic species, parallel with the first batch of germ cells embarking on the meiotic cycle, a substantial number of them remain in the gonial phase and constitute a portion of the reserve* at the expense of which the replenishment of the next batch of oocytes destined for spawning will take place (scheme 6).

In pink salmon, as also in other monocyclic species, the dependence of the ultimate on the potential fecundity is very clearly manifested and lends itself to precise study. In the polycyclic species, the potential fecundity must be reestablished at the beginning of each successive spawning

*The existence of a reserve of germ cells in animals is of exceptionally far-reaching importance and must be regarded as an adaptation developed in the course of evolution. It was shown in fruit flies that under the conditions of the experiment, the oogonia proved to be insensitive to the effects of radiation (Tikhomirova, 1967).

season. During the first reproductive cycle in polycyclic fishes (as opposed to monocyclic fishes), potential fecundity must be determined by the number of oocytes entering the protoplasmic growth period and destined for spawning. Thus, further study of the problem of the development of fecundity in fishes calls for a more detailed analysis of the mechanisms involved in the shaping, expenditure and replenishment of the reserve stock of germ cells.

A detailed study of the mechanism involved in the replenishment of the reserve stock should provide answers to many of the problems arising. In particular: what is it that regulates the involvement in the next cycle of oogenesis of only a portion of the oocytes and the resulting displacement of the growth phases of the oocytes from the antecedent to the subsequent? What is the role of gonadotropic and steroidal (sex) hormones in these phenomena? Of what value are the cells of the germinative epithelium in the replenishment of the stock of germ cells? 85

In the natural setting, with the change in the conditions of life of the species (table 23) and in the experiment (p.37), when they were irradiated by X-rays, in the females of the species a monotypical response reaction was obtained, namely a tendency towards an increase in fecundity. Such a reaction can be considered in terms of the "ecological aspect of stress"* (Bak and Aleksander, 1963; Mandel, 1964) to be the response of the population and the species to the developing unfavourable conditions. In certain circumstances the latter may lead merely to a temporary disruption of the germ cell development process, with a subsequent return to normal.

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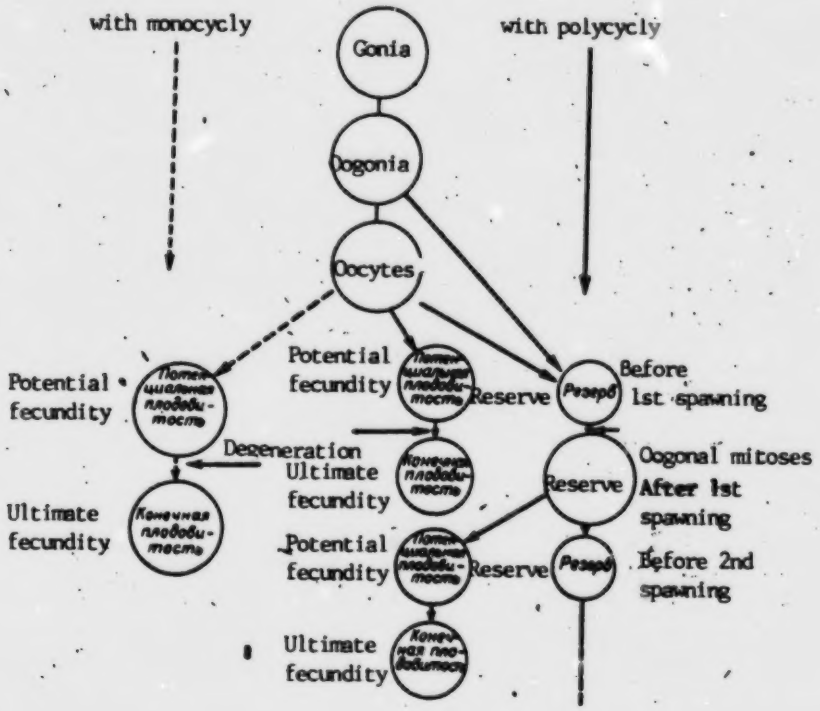
*It may be that the term "species stress" would be appropriate here, since it means the "programmed reaction of a species". In my opinion, this notion of species stress, suggested by M.A. Bobovich, a co-worker of our laboratory, correctly reflects the essence of the phenomenon being discussed.



Scheme 6. The formation of individual fecundity

CHAPTER 5 THE EARLY PERIOD OF GAMETOGENESIS UNDER CONDITIONS OF IONIZING RADIATION

86

The number of germ cells

With the exception of pink salmon, in all the species of the genus Oncorhynchus that have been studied, a direct path of sex differentiation has been discovered for both males and females: signs that the gonads are developing in either the male or female direction appear simultaneously. In the pink salmon, as mentioned earlier (p.45 of the original text - Tr.), we have encountered a different phenomenon.

A hypothesis has been advanced that a part of the pink salmon individuals possessing ovaries are males. Consequently, long before the beginning of gonadal redifferentiation there must exist two groups of fishes, similar in the anatomy of the gonads but dissimilar in sexual directivity. If the hypothesis is correct, then, based on the view that males and females are characterised by unlike sensitivities (Svetlov, 1943; Svetlov and Chekanovskaya, 1945, 1949; Levin, 1960; Patt and Brues, 1954; Annan, 1955; Rigo, 1964), given the extreme effect in the early period of gametogenesis, long before the beginning of a morphologically expressed sex differentiation, an unlike reaction on the part of the future males and females must be expected. Ionizing radiation was selected as the extreme factor.

For salmonids of the genus Oncorhynchus there are data on the use of both chronic and single exposures. No major deviations from the norm were detected in either the coho or the chinook salmon as a result of the action of Co^{-60} rays during the period from fertilisation to hatching at doses of 0.5 R/24 hrs (total dose of up to 40 R) (Donaldson and Bonham, 1964). In another experiment involving similar conditions of irradiation, chinook fry were spawned and released into the river. Several years later, the irradiated brood stock that had returned to the rivers to spawn were observed to have produced a larger number of eggs. The percentage of the brood stock returning also proved to be greater (Bonham and Donaldson, 1966). When experimental chinook fry underwent a single exposure to various doses, a retardation of growth was observed, although only in the variants where the dose exceeded 500 R (The Effects of X-Rays..., 1948), while in another study using the same subjects (The Effects of Roentgen Rays...., 1948), when irradiated with doses of 250 and 500 R the indices of mortality of the

embryos and the larvae were similar in the experiment and the control.*

In light of the published findings, in the present study 350 R was adopted as the basic dose for pink salmon.** The radiobiological effect (survival rate, growth rate, state and number of germ cells) were recorded a few days later, and subsequently on various dates, right up to 87
seven months after irradiation, by which time sex differentiation was already complete. Special attention was paid to those females in which, during the period following sex differentiation, the oocytes "constitute unique material for estimating the effect of the radiation at the cell level, since: (1) they are in about the same stage of the meiotic prophase; (2) death of cells due to radiation is typical of them, and (3) the reduction of their numbers cannot be restored by cell division" (Okberg and Klark, 1963, p.268). For the subject of the present investigation - pink salmon - this holds true to an even greater degree, since by virtue of monocycly, synchronicity in the development of germ cells is more pronounced in it than in polycyclic fishes.

It turned out that a dosage of about 1,000 R is sub-lethal in pink salmon. All of the larvae died within three months of being irradiated. In chinook salmon, with analogous conditions obtaining, a considerable percentage of the larvae died (52.5%) within a somewhat similar time frame - within 114 days of being irradiated (The Effects of Roentgen Rays..., 1948). At a dose of about 350 R the mortality indices of the pink salmon embryos and larvae, and also the growth rates in the experimental and control groups were almost the same. However, the number of germ cells

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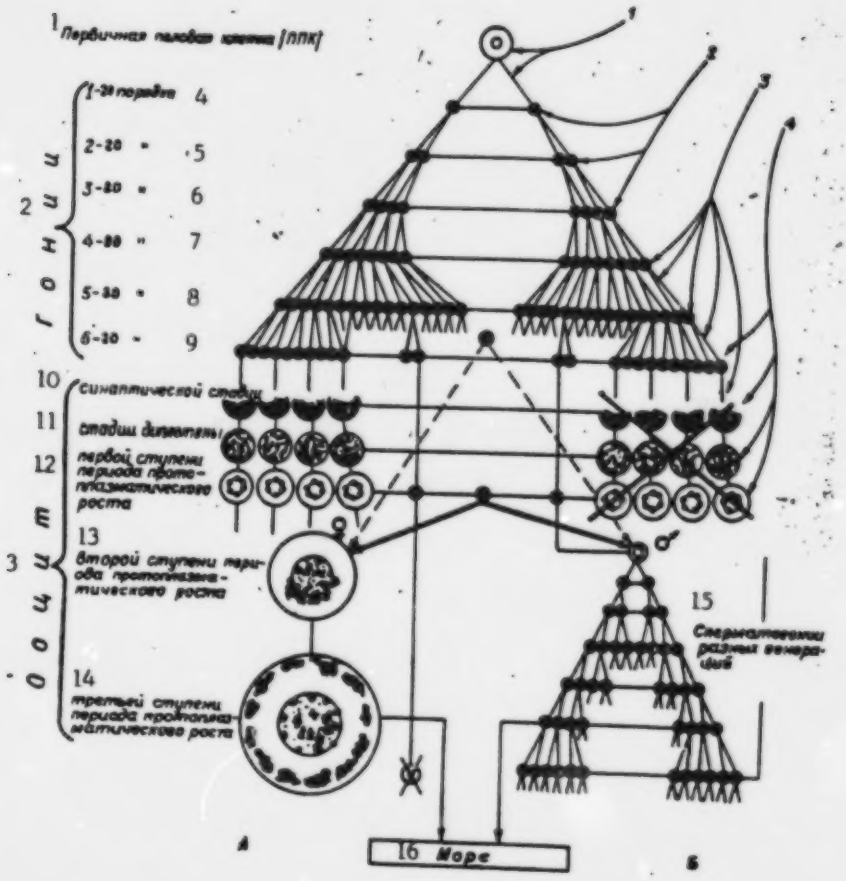
*Data pertaining to aspects of the morphology and gonadal function of animals under conditions of ionizing radiation are presented in review articles and special manuals (Golovinskaya and Romashov, 1958; Raf, 1962; Klemedson and Nel'son, 1962; Zakutinskii, 1963; Li, 1963; Carlson and Cassner, 1964; Mandl, 1964; Karapetyan and Vardanyan, 1967).

**I am deeply grateful to Lyudmila Alekseevna Kashchenko for her advice at the time of working out the schematic diagram of the experiment.

Apparently transliterated into the Cyrillic from Oakberg and Clark (Tr.)

differed substantially. This is most fully traced in the results of the experiment in which the dosage in each of the four variants was identical (about 350 R) and the initial condition of the germ cells at the time of irradiation was different in each of the variants. In the first variant, only PGCs were present in the gonads, and they had either not yet undergone mitotic division or had only just begun to exist. In the second variant - PGCs were no longer seen, but there was a fairly large number of gonia, apparently still of the first orders only. In the third variant, besides a large number of gonia of different orders, solitary oocytes of the synaptic stage were encountered. In the fourth variant, a large number of the oocytes were already in the diplotene stage (scheme 7) during the period of exposure.

Between five and seven months after irradiation, in comparison with the control group, the average number of germ cells in the experimental females was as follows: 315% in the first variant; 202% in the second; 176% in the third; and 74% in the fourth. In the males the number of spermatogonia (during this period of development there are no other generative cells in the testes) was as follows: 143% in the first variant; 103% in the second. In terms of the spermatogonia count the males of the third variant can be divided into two groups. In two of the males there was an average of 1,506 spermatogonia (1,279-1,734), and in three of them - an average of 74 (14-159). The first group is accordingly regarded as variant 3a, the second group - as variant 3b. In the fourth variant the testes proved to be almost sterile. Consequently, by the time that the radiobiological effect was calculated the reactions of the males and the females to irradiation were dissimilar. 88



Scheme 7. Gametogenesis of pink salmon embryos, larvae and fry in the river period of life. Initial condition of the germ cells in the different variants of the irradiation experiment.

Key: 1. Primordial germ cells (PGCs). 2. Gonia. 3. Oocytes.
4. Of the 1st order. 5. Of the 2nd order. 6. Of the 3rd order.
7. Of the 4th order. 8. Of the 5th order. 9. Of the 6th order.
10. Of the synaptic stage. 11. Of the diplotene stage.
12. Of the first phase of the protoplasmic growth period.
13. Of the second phase of the protoplasmic growth period.
14. Of the third phase of the protoplasmic growth period.
15. Spermatogonia of various generations. 16. Sea.

A - development of germ cells in the females; B - development of germ cells in the males. The cancelled out portion denotes that total degeneration of the germ cells in the given condition is occurring. The two solid lines indicate the moment when morphological indices make it possible to decide whether a particular individual is developing in the male or female direction,

Scheme 7 (Cont'd)

which essentially means forming a judgment on the completion of the sex differentiation process. The broken line indicates the same moment which, however, was revealed experimentally to be much earlier than that which was based on morphological characters. The arrows numbered 1, 2, 3, 4 indicate the moment of irradiation. The single arrow characterises the condition of the germ cells in the males and females during the period of their migration from the rivers to the sea.

The dissimilar reaction to irradiation on the part of the males and 89
females in the experiment is also confirmed when analysing the other parameters. Of major interest in this context is the comparison of the indices characterising the ratio between the numbers of germ cells in the males and females in the experimental variants and in the control. In the control it amounted to 93%, and in variants 1 and 2 it was almost 50% lower. In the third variant, in part of the males (variant 3a) this ratio was also 50% lower than in the control, but in another part of the males (variant 3b), as also in variant 4, the ratio between the numbers of germ cells in the males and females was no more than 2 to 3 % (table 24). Also attesting to disparities between the males and females are data on the amplitude of individual fluctuations in the numbers of germ cells in the experiment and the control. In the females the ratio between the minimal and maximal numbers of oocytes was 0.676:1 in the control. However, it was 10 times greater in the experiment. The fluctuations were seen to be much more pronounced in the males. The ratio between the minimal and maximal numbers of spermatogonia was 0.176:1 in the control, whereas in the experiment the amplitude of the fluctuations was almost 100 times greater.

Table 24

Number of germ cells in pink salmon males and females at the moment of terminating the experiment

1 Пол	2 Контроль	3 Вариант опыта				
		1	2	3 а	3 б	4
♂	1746(8)	2503(2)	1800(3)	1506(2)	74(3)	48(3)
♀	1866(13)	5888(3)	3772(6)	3302(2)	3302(2)	1393(5)
	93%	42%	48%	45%	2%	3%

4 Примечание. Без скобок указано число половых клеток, в скобках — число особей; то и другое — в абсолютных цифрах. В процентах показано отношение количества половых клеток у самцов к количеству половых клеток у самок. Объяснение вариантов 3 а и 3 б см. в тексте (с. 87).

Key: 1. Sex. 2. Control. 3. Variant of experiment. 4. Note. The number of individuals is indicated in brackets, the number of germ cells - without brackets. Both values are given in absolute figures. The ratios between the numbers of germ cells in the males and females are shown as percentages. For an explanation of variants 3a and 3b see p.35.

When assessing the results of the irradiation experiment, attention is drawn to the fact that, in comparison with the control, the number of germ cells is higher in pink salmon females when exposed to irradiation and under the conditions of their acclimatisation in the Arctic. Thus, one and the same effect was obtained under dissimilar conditions: during acclimatisation (Persov, 1963b), i.e., without experimental irradiation, and subsequent to irradiation in the experiment (the findings of the present study).

It was difficult to estimate the sex ratio in the experiment, since the number of individuals used in the study proved to be insufficient for the purpose of obtaining statistically reliable information. However, the very fact that males appeared on approximately the same dates as in the 90
control group affords a basis for postulating that the sex differentiation after irradiation
process/in the experimental fishes was closely similar to that in the

control group (Persov, 1967a). Also well documented, however, is certain other information relating to fishes, such as, for example, when exposure to radioactive phosphorus led to retardation in sex differentiation (Vivien, 1952).

When analysing the radiation effect on the reproductive system, an important index is the age of the individual. In many instances, the condition of the germ cells will depend on this. By taking age into consideration it accordingly becomes possible to obtain an advance indication of a particular effect of the irradiation (Frits-Niggli, 1961; Oster, 1963; Amorozo, 1965). Although this also holds true in the general sense for fishes, it must be remembered that the duration of the embryonic period in them is in large measure dependent on the temperature conditions.

In the present study, rather than the absolute age of the embryos and larvae in days, a more convenient and more comparable index was found to be the relative index, expressed as a percentage of the total number of days during the entire incubation period. For example, if the age of an embryo is 56 days after fertilisation, in relative indices it will be 79%. By knowing the length of the incubation period (at a given temperature this will be a relatively constant value), it becomes possible to calculate in advance (depending on the conditions of the experiment) when would be the most expedient time to do the irradiating.

In analysing the results of the experiment it is important to know the duration of the separate stages of gametogenesis. Observations performed on one and the same batch of fishes make it possible to determine these time frames as a first approximation. Thus, in pink salmon PGCs were discovered over a period lasting 10 days (from the 9th to the 19th day after fertilisation). The first gonia were found on the 19th day, and the

first oocytes of the synaptic stage - on the 39th day. Consequently, the gonial stage lasted about 20 days. By knowing the number of primordial germ cells present at the start of gonadal development (50), the number of gonia by the time meiosis began (3,000) and the time span during which an increase was occurring in the number of germ cells (20 days), a precise determination could be made of the number of cell generations and the duration of one mitotic cycle of the gonia calculated, which in the present case (given the synchronicity of the divisions) could be equated to approximately 3.5 days.

Duration of indifferent period

As indicated earlier, sex differentiation is discovered morphologically, either from the time of appearance of anatomical differences in the structure of the gonads (anatomical sex differentiation) or from the time of appearance of germ cells in the stages of the meiotic prophase - the preleptonema, leptonema and zygonema stages (cytological sex differentiation). Here, as already mentioned, two variants are possible. In the first of these, which is the most prevalent, differences in the condition of the gonads - their development in the male or female direction - are manifested simultaneously. In the second - gonadal development in all the individuals is initially in the direction of one sex only (protandry, protogyny). Representatives of the other sex can only be found after re-differentiation of the gonads has occurred in part of the individuals, In the second variant, sex differentiation extends over a longer time frame. 91

Even before the experiments relating to the effect of ionizing radiation were conducted it was clear that the answer to the question of the duration of the indifferent period could only be obtained in the case

of low-dose exposures which did not give rise to a disturbance of the basic functions of the organism, but at the same time were capable of influencing the course of development of the gonads.* The special character of the subject made it impossible to trace the development of the pink salmon over its entire life span (including the reproductive period). Accordingly, the calculation based on the results of the exposure, made during the 5th - 7th month of age, must be regarded as an index characterising the condition in only one of the stages of the life cycle - when the fry are making the transition from the river to the sea mode of life. It is during this period that the process leading to testes formation in the males takes place. In the testes, only spermatogonia of dissimilar cell generations are found, while in the ovaries of the females there are oocytes of mainly the second and third stages of the protoplasmic growth period (scheme 7).

The derived information makes it possible to conclude that in pink salmon the germ cell differentiation process begins earlier than the time when this could be judged to have occurred on the basis of morphological data. The results of employing certain agents, for example, ionizing radiation, confirm the earlier (still in the pregonadal** period) differentiation of the germ cells in the male or the female direction. With the transition of the germ cells to meiosis, this process, which had long since begun, is merely completed.

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* A review of the results of studies aimed at revealing the stimulating effect of low doses of ionizing radiation on oogenesis is contained in a book by S.K. Karapetyan and V.A. Vardanyan (1967).

** It remains an open question as to whether the sexual tendency of the gametes can be identified even earlier. Judging from the data with respect to other animals (Rana esculenta - Padoa, 1963, 1964), a negative answer must be expected.

The gonia of the various cell generations react to irradiation in different ways. As is well known, there are two types of spermatogonia in the males: the reserve types "A" and the active types "B" (Kashchenko et al., 1960; Frits-Niggli, 1961). There are indications that in mice it is not only the reserve and active spermatogonia that differ in radiation sensitivity, but also all four populations of type "A" spermatogonia (Mounzi, 1963). The literature also contains a reference to maximum radiosensitivity of the spermatogonia of the premeiotic generation (Mandl, 1964). 92
The experimental findings of the present study (scheme 7) also confirm that the sexual tendency of the gametes in the course of gametogenesis, for example, the spermatogonia, is dissimilar. This shows up well in the characterisation of the post-radiation condition of the germ cells.

Acknowledgement that the cell populations of the gonia are non-equivalent in turn requires that a more profound understanding be gained of the role played by a number of the endocrine organs associated with the reproductive system in the achievement of the sex differentiation process (Persov, 1967a). It is possible that, as sex individuation proceeds, there is a decline in the relative autonomy of gonadal development and a gradual increase in the regulatory role of the organism, especially by the time the germ cells make the transition to a definitive path of development.

The transition from mitotic cycles to the meiotic cycle*

The foregoing data can be used for a special discussion of an important stage in the sex differentiation process in fishes - the moment when the gonia make the transition to the meiotic cycle. In moving towards a schematisation of our ideas it can be taken for granted that during the period of mitotic divisions of the gonia, the mechanisms of development are accomplished chiefly at the cell** level, and during the transition to the meiotic cycle - at the level of the organism. On this basis, it is easy to see why the gonia of the earlier orders continue to divide and do not make the transition to the meiotic cycle (the organism is not yet ready for completion of the sex differentiation process).

In the course of gametogenesis, the germ cells of pink salmon pass through two successive stages: proliferation and specialisation (definitive development). Grouped within the first stage are PGCs and gonia of the period of mitotic divisions, which in the case of pink salmon, is from the first to the fifth cell generations inclusively (scheme 7). The second stage of their development begins at the moment when the cells make the transition to the meiotic cycle. Proliferation of the primordial germ cells is possibly stimulated by substances closely similar to those which, according 93
to published data, are responsible for the first divisions of blastomeres and are regarded as "anteneural mediators" (Buznikov, 1966).

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* The term "meiotic cycle" must evidently be accepted with some reserve, since the beginning of this cycle, as distinct from the mitotic cycle, undoubtedly marks the transition of the cell to the definitive path of its development. This can be illustrated by reference to the development of oogonia and spermatogonia from the so-called reserve stock, which is possible in one direction only - that of oocytes or spermatocytes.

** In the periods characterised by the beginning of migration and concentration of PGCs the gonads are still absent. This is the pre-gonadal stage (scheme 5). The beginning of gonad formation coincides with the first mitotic divisions of the PGCs. Consequently, in this stage of gametogenesis a relatively greater autonomy of the germ cells can be observed than, for example, in the period the sex differentiation process is being completed.

In interpreting the absence of the necessary conditions for making the transition to the next cycle as a form of blocking, one can conceive of the germ cells in pink salmon being blocked twice during the period prior to sex differentiation. The first blocking is operative for a period of 10 days, after which the cell division period sets in. This occupies about 20 days and it is during this period that the second blocking action is observed, when the transition to the meiotic cycle of the 1st-5th order gonia is delayed and becomes possible only for gonia of the sixth order.

In somatic cells, emergence from the mitotic cycle does not necessarily signify specialisation of the cell. It may be related to a lengthening or a change in the relationship between the separate phases of the cycle (Zarvarzin and Lebedeva, 1964; Dondua and Fedorova, 1964) and may consequently be temporary (Dondua and Fedorova, 1964). To what extent are these observations applicable to germ cells? The question is complicated and I therefore deliberately wanted to pose it in a form that is more specific than general: to what extent are these observations characteristic of germ cells of the sex differentiation period in animals with a single process of reproduction, such as monocyclic fishes? This question is best discussed separately for males and females.

In females of monocyclic species of fishes the emergence of oogonia from the last mitotic cycle and the transition to meiosis occur only once. In them there is no reserve stock of oogonia and there is practically no interruption between the last mitotic cycle and the beginning of the meiotic cycle. Consequently, one cannot expect a temporary emergence of oogonia from the mitotic cycle, as is known to be the case with somatic cells.

In comparison with females, in males of monocyclic species (such as the Pacific salmons) the transition to meiosis is delayed by many months,* when a rapid increase in the number of spermatogonia occurs due to mitotic divisions. In males it is therefore more complicated to calculate the number of cell generations, and hence more difficult to determine how immediate is the transition of the spermatogonia from the last mitotic cycle to meiosis. The solving of these problems is even more laborious for animals with a polycyclic type of reproduction, in which the expenditure and replenisment of the reserve stock of germ cells occurs repeatedly. It would be preferable for such problems to be resolved on model subjects, which should include fishes with a monocyclic type of reproduction.

Disorders in the hormonal regulation of gametogenesis

A fairly large amount of information is now available on the role of the endocrine system in regulating the maturation of male and female germ cells (see for example, one of the latest summaries devoted to mammals - Savchenko, 1967, and an analogous summary pertaining to fishes - Picford and Atz, 1957). Therefore, when studying the function of the gonads under conditions of ionizing radiation, great importance is attached to the study of the "adenohypophysial-gonad" system. It has been found that when subjected to radiation the gonads lose their sensitivity to "hormonal stimulants" and that in the adenohypophysis a "blocking of hormonal secretion" occurs. It was based on this that the hypothesis concerning "radiation induced disintegration of the endocrine system", which had been traced in a number of animal species, was formulated (Kashchenko, 1962, 1963, 1965, 1971; Kashchenko, 1965; Radiation Endocrinology, 1967). Problems arising

*It may be noted that this circumstance creates favourable conditions for studying the experimental effects.

when studying the state of the endocrine system in the post-radiation period have been treated in detail in a special review of the literature (Prokudina, 1965).

The importance of the endocrine system in controlling post-radiation gonadal function was demonstrated in the Japanese fish Oryzias latipes. Irradiation retarded the section* of the gonadotropins, which led to delayed development of the ovaries. Implanting of pituitary tissue weakened the effect of the irradiation in that the development of the ovaries approximated to normal (Egami and Hyodo, 1965). Consequently, the effect of irradiation on gonad development in O. latipes took the form of damage to the endocrine bonds. Recently, interesting results were obtained in loaches. In comparison with the control group, a double dose of pituitary extract was required by the females for a roe to be obtained by the hypophysial injection method. This was regarded as the result of "damage to the hormonal system" (Shekhanova and Penkurenkov, 1969, p.349). The correlation existing in fishes between the gonads, the pituitary gland, the adrenals and the other organs of the endocrine system is analagous to that obtaining in the higher vertebrates (Picford and Atz, 1957; Bern and Nandi, 1964; Hoar, 1965; Sundararaj and Goswami, 1966). This makes it possible to apply the concept of "radiation induced disintegration of the endocrine system" to the fishes as well.

In the present work an attempt is made to ascertain the effect of low doses of X-rays on the development of the reproductive system, by taking hormonal factors into consideration. It is shown that in those cases in which only PGCs were present in the gonads at the time of irradiation,

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*From the Russian word 'sektsiya', the meaning of which is not clear in this context (Tr.).

in the irradiated females the number of oocytes was larger. This increase presupposes the existence of a larger number of gonia, even prior to the beginning of meiosis, than in the control group. In other words, subsequent to irradiation the number of cell generations of the gonia must have been greater. What could have accounted for this increase? Two possibilities appear to be the most likely: either it occurred through a shortening of 95
the duration of each of the mitotic cycles (Tsanev and Markov, 1964) or, as is maintained in this book, through a lengthening of the gonial proliferation period with a constant duration of each mitotic cycle. In both cases the number of gonia in the females of the experimental variants must have increased.

In the literature devoted to the development of germ cells attention is focused mainly on the mitotic cycles, to a lesser degree on the meiotic cycle, and less still, on the transition from the former to the latter. This is attributable to procedural difficulties in selecting a model subject with a relatively synchronous development of germ cells and a monocyclic development of gonads. It is clear that these circumstances have limited the scope of the research on this problem in fishes (the situation is slightly better in other classes of vertebrate animals).

In the main, DNA synthesis in the meiotic cycle is completed during the pre-meiotic prophase* (Prokof'eva - Bel'govskaya, 1960; Kemp, 1964; Utakoji, 1966; Ivens, 1966). Therefore, having regard to the known scheme of the mitotic cycle (Epifanova, 1962, 1965; Meziya, 1963; Tsanev and Markov, 1964), it is to be expected that with the transition to meiosis the gonia of the last cell generation will pass from the G_1 mitotic phase to the S phase of the meiotic cycle (scheme 8).

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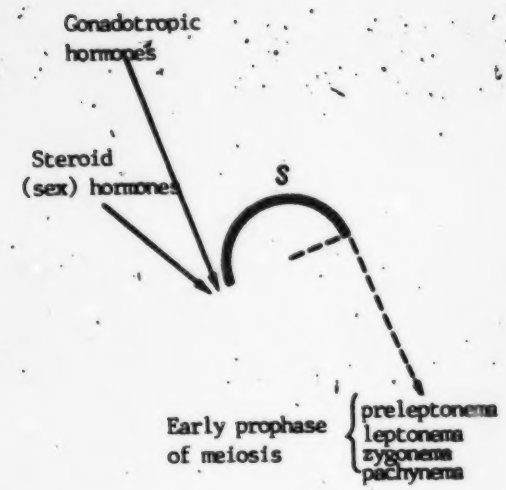
*In the meiotic cycle of mice, DNA synthesis is observed twice, on the second occasion - on completion of the process (Sirlin and Edwards, 1959).



Scheme 8. Transition from the mitotic cycles to the meiotic cycle in the sex differentiation process. According to Ivens (1966), the early meiotic prophase corresponds to G2 of the mitotic cycle.

In fishes maturing for the first time the transition to the 96
completion of the sex differentiation process (in the case under discussion it is precisely this that denotes the transition from the mitotic cycles to the meiotic) is evidently dictated by the influence of the gonadotropic and steroid (sex*) hormones.

The positive role of the gonadotropins in early gametogenesis can be judged from the action of purified gonadotropic hormones. In Lacerta vivipara it proved possible to cause feminisation with such hormones (Dufaur, 1965). After administering purified gonadotropin hormones of pigs (FSH) and sheep (LH) to Bufo arenaruim at the age of one month after metamorphosis, through the action of the follicle stimulating hormone 100%

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*In one of the most recent studies it is emphasised that the transition from the mitotic cycles to the meiotic is accomplished "under the influence of the sex hormones" (Bogdanov, 1971).

males were obtained, and through the action of the luteinising hormone - 100% females (Burgos and Pisano, 1959). Furthermore, it has been shown that hypophysectomy in B. americanus does not affect embryonic sex differentiation (Chin ve Chang, 1955).

More precise data on the role of gonadotropic hormones in early ontogeny exist for man. As in many animal species, in man PGCs migrate from the region of the vitelline entoderm to the region of future gonadal establishment and thus prove to be constituent members of the cells of the coelomic epithelium. In the gonadal region the latter is known as the germinative, generative, germinal or rudimentary epithelium. At a certain stage of development, epithelial strands form in the zone where the germ cells are, due to the so-called "immersion growth" (Knorre, 1959). At two months of age, anatomical differentiation of the gonads occurs in human embryos and by the age of five months, germ cell differentiation is observed.

The transition to meiosis and folliculogenesis in female embryos coincides in time with the production of FSH and LH (Levina, 1966, 1973, 1974; Levina and Ivanova, 1966; Ivanova and Levina, 1966; Volodina, 1966; Dainenko, 1967; Borisova, 1968). It would have been interesting to monitor the state of the pituitary gland at the beginning of active spermatogenesis, which in boys occurs in the post-natal period. Possibly it would have been found to be analogous to the state of the gland in female embryos during the transition to oogenesis. In that event there would have been no fundamental difference between male and female individuals in the realization of cytological sex differentiation and the hormonal control of it: in females this is detected in the prenatal and in males, in the post-natal periods of development.

Some experimental data on the role of gonadotropins in the realization of the sex differentiation process are also available for the fishes. In males of the flounder Pleuronectes platessa, for example, the transition from spermatogonia to spermatocytes is controlled by the pituitary. This was ascertained by hypophysectomy and subsequent stimulation by gonadotropins* (Barr, 1963). In one of the representatives of the salmonid fishes - Salmo gairdnerii - the beginning of spermatogenesis was induced by injections of pituitary extracts (Pituitary Hormones..., 1965). In the goldfish Carassius auratus, reproduction of oogonia was disrupted by hypophysectomy, but upon the supplementary introduction of gonadotropins, this process occurring immediately prior to meiosis, was stimulated (Yamazaki, 1965). In Couesius plumbeus, hypophysectomy had the effect of suppressing the spermatogonia reproduction process and of totally blocking their transition to spermatocytes (Ahsan, 1966). The literature also contains data on trout and cisco with respect to coincidences in the times of appearance of basophilia in the cells of the pituitary gland and to sex differentiation (Kerr, 1940). Even less information is available on the role of adrenal steroid hormones** in the sex differentiation process than that which deals with the importance of the gonadotropins. 97

The existing information, however sparse, makes it possible to evaluate the endocrine system of fishes as a potential regulator of the

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*It is necessary to point out that, when used in conjunction with hormonal therapy, the hypothysectomy procedure can be successfully utilised in fishes with a protracted indifferent period. In sturgeons, in which the indifferent period lasts for more than a year, a procedure for surgical removal of the pituitary gland has already been developed (Zubova, 1971a).

**Detailed information on the analogy between the adrenals of mammals and the anterior interrenal tissue of fishes is presented in a monograph devoted to a study of the endocrine system of Fundulus heteroclitus (Picford, 1959).

mechanism whereby germ cells make the transition to the meiocyte state. We believe that the enhanced production of gonial cell generations in pink salmon under the influence of irradiation is the result of a more protracted blocking of the transition of the germ cells from the mitotic cycles to the meiotic. The suggested delay, in our view, is attributable to the later inclusion as regulators in the sex differentiation process, of gonadotropins and steroid sex hormones (Persov, 1967b,c). Thus, from the standpoint of this hypothesis, total irradiation of embryos and larvae leads to inhibition of certain of the endocrine organs and their temporary "disintegration" (Kashchenko, 1962, 1963, 1965; Voitkevich, 1967). Eventually, this leads to a delay in the beginning of the meiotic cycle and consequently, to an increase in the number of germ cells.* As a result, conditions may subsequently be established which are conducive to an enhancement of fecundity in the females.

Also possible is another assessment of the experimental findings. The transition from the mitotic to the meiotic cycle is the beginning of the path of definitive development of the germ cells. It therefore has 98
much in common with the transition of somatic cells to the differentiated state, which is illustrated by findings for various groups of animals (Cambar, 1956; Nadjioloff et al., 1962; Fedecka-Breener, 1967). Unquestionably, the regulating of these phenomena in the different stages of ontogeny must have common foundations. The position taken by authors working with invertebrate animals is even more decisive on this question. According to their ideas, the differentiation of germ cells is in no way different from that of somatic cells (Brian, 1968; Stefan-Dyubua, 1968).

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*With a view to obtaining a clearer understanding of the blocking and deblocking mechanism in the transition to meiosis, published findings on the retardation of this process in male insects by the action of Actinomycin "D" (Jain, Umrae Singh, 1967), with a parallel prolongation of the mitotic cycles, may be consulted.

Thus, in studying the influence of radiation factors on the development of germ cells it is necessary to take into account a specific property which is typical of gametogenesis: replacement of the mitotic cycles by the meiotic. In the course of ontogeny this replacement denotes that the sex differentiation process has been completed

Recovery of the structure and function of the gonads

When analysing the course of restoration of gonadal structure and function the first question that arises concerns the sources of this restoration. The problem of gonad restoration after irradiation is closely linked to the question of the origination of definitive germ cells. Various ideas are extant here and in particular, evidence is adduced in favour of the active participation in this process of the cells of the germinative epithelium. Possible sources of restoration of the testes in post-irradiation males are Sertoli's cells (Schinz and Slotopolsky, 1925) and type "A" spermatogonia (Kashchenko et al., 1960; Oakberg, 1955). In females subjected to irradiation, this question has not been studied as extensively.

In assessing the course of restoration of the gonads extreme caution is needed, since morphological restoration (the observations were on mice) may be accompanied by an abrupt fall in functional capacity for reproduction (Amorozo, 1965). In general, the problem of fecundity is one of the most important when analysing post-radiation results. In a very general sense it can be noted that an increase in dosages leads a decrease in fecundity, for example, in Drosophila robusta, at 2500 R fecundity is restored 16 days after irradiation, but when the dosage is doubled, fecundity continues to be sharply depressed (Annan, 1955). An analogous observation was recorded

with rats, the fecundity of which began to decline when the total radiation dose was increased (Ingram, 1958). Of fundamental importance is the state of the reproductive system at the instant of exposure. In the rats, the abrupt fall in fecundity set in only in the event that irradiation was maintained until the 16th day of pregnancy (Beaumont, 1962), which coincides with an episode of oogonial mitoses (Mandl, Beaumont, 1964). In man, the most dangerous period is between weeks three and six of pregnancy (Gifarelli, 1963), that is, the period in which an active process of organogenesis is taking place. In other cases, with respect to 99 fecundity, ontogeny cannot generally be confined to the most radio-sensitive and radio-resistant periods (Baker, Beaumont, 1967). The increase in fecundity which is sometimes observed after irradiation may only be transient. For example, in the white mouse the number of maturing follicles increases with acute radiation sickness. They are, however, inevitably destined to degenerate (Karmysheva, 1963).

Instances of a sharp drop in fecundity subsequent to irradiation have also been recorded for fishes (Samokhvalova, 1935, 1938). The observed decrease may prove to be temporary, with the original fecundity being restored later. This was discovered, for example, in Lebistes reticulatus (Natali, 1940,a,b) and in Oryzias latipes (Solberg, 1938). In the latter fish, which inhabits the Japanese rice fields, the lowering and subsequent restoration of fecundity, depending on the dosage, have been traced in detail. At 2000 R, in the first two weeks the number of germ cells remains equal to that of the control group. During the next four weeks it drops abruptly, and yet two weeks later it again becomes equal to the control. At a dosage of 8000 R, 5 days after irradiation the number of oocytes

decreases sharply and is not restored subsequently (On the Influence...., 1955). Apparently, the absence of sufficiently objective indices of the state of the recipient at the moment of radiation exposure leads to dissimilar and, at times, opposite assessments. When Lebistes reticulatus is irradiated prior to attaining one month of age, notwithstanding published findings, gametogenesis is not restored, even as long as four months after irradiation (Vivien, 1953).

The decisive importance of the initial state of the gonads at the instant of irradiation was demonstrated in the South African fish Tilapia mossambica. According to a number of indices, including fecundity, different post-radiation effects were recorded upon irradiating the larvae at the ages of 6, 13 and 27 days, at which times, respectively: only PGCs were present, or mitotic reproduction of germ cells, prior to sex differentiation, occurred, or sex differentiation had already taken place and oocytes were seen in the females (Fam Man' Chung, 1970). The findings of that study are convincing, as the author had succeeded in tracing the post-radiation effect in two generations.

Restoration of gonadal function in fishes may sometimes be accompanied by the formation of hermaphroditic gonads (Egami, 1955, 1956; Telitchenko, 1958; Cherfas, 1962). Ionizing radiation can also lead to inactivation of the spermatozoids and eventually to radiation gynogenesis (Romashov, Golovinskaya, 1960; Romashov et al., 1960; Romashov and Belyaeva, 1964, 1966; Vasileva-Dryanovska and Belcheva, 1965; Rugh and Clugston, 1955). In any discussion of such matters, the results of research on radiation-induced chromosome damage must naturally be taken into consideration (Ivens, 1966; Sperrou and Vudvell, 1968; Tsankova, 1965). Of independent interest

are studies aimed at gaining a more precise understanding of the role of gonadotropins in gonal reaction at the instant of irradiation and* in the post-radiation period (Persov, 1967c).

In the present work the question of providing a survey of all of the sections concerned with the irradiation of fishes has not been raised. However, certain aspects of these phenomena which are important in assessing the effect of ionizing radiation on the gonads, must be mentioned. For example, it was found that irradiation has an inhibiting effect on gametogenesis when gonadogenesis is progressing normally (Marin, 1959). In assessing the results of radiation exposure it is essential that temperature conditions are taken into account (Bonet-Maury, 1963), since it is probable that in certain cases, they may help to explain peculiarities in the post-radiation condition of the gonads. For example during the post-radiation period Oryzias latipes dies within 20 days at temperatures of 20-25°, but lives for more than four months at a temperature of 6° (Etoh and Egami, 1965). At optimal temperatures the flounder dies more rapidly after radiation (Ivanov, 1966), while the guppy becomes more radiosensitive (Tsugava and Yamamoto, 1962).

Of definite interest are data on the accumulation of certain radioactive elements** in the course of ontogeny. In carp fry, strontium -90 accumulates ten times more actively than it does in carp yearlings (Lebedeva, 1961). In adult carp, P^{32} accumulates particularly actively in the course of vitellogenesis and in the pre-ovulation period (Irikhimovich and Zelenin, 1961). Apparently, the question of the lesser sensitivty of germ cells

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*Conjunction inserted (Tr.).

**Detailed information is presented in one of the first reports dealing with radioecology of marine organisms (Polikarpov, 1964).

calls for further examination, since in Macropodus opercularis, for example, the blood and blood-forming organs were found to be the most radiosensitive, followed by the eyes, the CNS and, finally, the germ cells (Allen and Mulkay, 1960).

At the time of writing, the question of the effect of radiation, particularly chronic irradiation, on the development of PGCs throughout the post-radiation period, has still not received adequate attention. Of great interest in this connection are data derived by I.P. Migalovskii (1971). The author traced the radiation effect in Atlantic salmon embryos from the 80th to the 231st day after fertilisation, which enabled him to characterise the dynamics of change of a number of primordial germ cells (table 25).

As will be seen from the data in table 25, in all of the concentrations (2×10^{-5}; 0.7×10^{-6}; 0.6×10^{-7}) the process of gametogenesis was seen to be inhibited, but at 0.6×10^{-7} the reparative process began earlier than in the other variants and was so intensive that the number of PGCs proved to be greatest in that variant. At 0.7×10^{-6}, inhibition 102
was less pronounced and the onset of the reparative process occurred later. At 2×10^{-5}, the inhibition proved to be so pronounced that during the period of the observations (from the 80th to the 231st day after fertilisation) the reparative process did not set in at all.

Thus, there are grounds for believing that the dosages used in the cited study are primarily effective in suppressing the mechanism of reparation (Strelin, 1966). Depending on the dose, the lessening of the inhibitory effect occurs at different times (for the 2×10^{-5} variant the reduction of this effect should probably be expected even later, i.e. after the 231st day).

Table 25

Number of PGCs according to periods of development (after Migalovskii, 1971) 101

1 Варианты	2 Активность икры (кюри/икринка)	3 80 дней после оплодотворения		4 102 дня после оплодотворения		5 231 день после оплодотворения	
		6 число ППК	t_{diff}	6 число ППК	t_{diff}	6 число ППК	t_{diff}
7 Контроль	0	44,6±7,23	—	47,6±3,61	—	65,9±8,52	—
8 Sr^{90}—Y^{90}; 2.10^{-5} *Кюри/л*	$1,8 \cdot 10^{-8}$	26,3±4,24	2,18	32,6±2,02	3,63	34,6±5,00	3,17
9 Комбинированный	$1,8 \cdot 10^{-8}$	22,4±3,35	2,81	29,0±3,00	3,95	33,9±3,99	3,40
8 Sr^{90}—Y^{90}; $0,7.10^{-6}$ *Кюри/л*	$2,8 \cdot 10^{-10}$	39,3±4,30	0,63	43,3±3,20	0,89	63,7±10,69	0,16
8 Sr^{90}—Y^{90}; $0,6.10^{-7}$ *Кюри/л*	$5,8 \cdot 10^{-11}$	30,3±3,45	1,78	51,2±7,95	0,41	72,5±8,01	0,56

Key: 1. Variants. 2. Activity of egg (Curies/ovum). 3. 80 days after fertilisation. 4. 102 days after fertilisation. 5. 231 days after fertilisation. 6. Number of PGCs. 7. Control. 8. Curies/ 9. Combined.

Of major interest are the dynamics of the indices of the number 102
of germ cells in the 0.6×10^{-7} variant, in which the inhibition was replaced by a rise, and later an excess of the number of PGCs over the control group. It would seem that what we are encountering here is the action of two opposing radiation effects - suppression of the reparative processes and stimulation of gametogenesis, with the latter effect only becoming operative after a lessening of inhibition.

Hence, the hypothesis regarding the dual effect of ionizing radiation and (arising from this) the dissimilar mechanisms resulting in the germ cells of the early period of gametogenesis being both inhibited and stimulated, appears to be valid.

Detailed research on the effects of low doses of irradiation on animals is bound to be of major interest. Compared to plants,* it is obvious that insufficient attention has been paid to irradiated animals. Meanwhile, judging from certain of the findings, investigations of this nature, particularly when performed with fishes, may hold considerable promise. For example, when irradiating Tilapia spp., in some variants there was an enhancement of fecundity, in others - of the growth rate (Fam Man Chung, 1970). Thus, through experimentation the author succeeded in separating the processes directly associated with reproduction and the processes associated with the growth rate. Also, some very interesting data were derived from experiments on Tilapia, although not in terms of external irradiation, as was the case in the Fam Man Chung experiments,

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*Research relating to hydrobionts should be organized similarly to the manner in which it is conducted in plants, when reactions to radiation effects are studied in the natural coenoses (Plett, 1968; Vudvell and Osting, 1968). We fully concur with the view that such concepts as "Ecological radiosensitivity", "irradiation-induced damage to the biocoenosis," and "radiation biogeocoenology" (Aleksakhin, 1968) should be brought into general use.

but with implanted irradiation using radiostrontium (Sr^{90}-Y^{90}). The relationship between the growth rate and the rate of maturation in solutions with a differing concentration proved to be variable (Voronina, 1972). Thus, at 1×10^{-10}, accelerated growth was accompanied by maturation remaining at the level of the control fishes. At a concentration of 1×10^{-8}, retardation of Tilapia growth occurred in parallel with an acceleration of its maturation, and at a concentration of 1×10^{-6}, a very high growth rate coincided with an observed delay in the start of the spawing run by the females.

CONCLUSIONS

In the early stage of gametogenesis and gonadogenesis, of special 103
interest are such phenomena as the migration and concentration of primordial germ cells; the establishment of the gonads; the start of mitotic divisions of the PGCs and gonia of subsequent orders; the transition from the indifferent state of the gonads to their differentiation, both in the structural sense and with respect to cell composition (anatomical and cytological differentiation of the gonads respectively).

Long before the emergence of morphological indices of sexual directivity in the development of germ cells it is possible through the influence of ionizing radiation to produce a dissimilar reaction of the germ cells, as a function of their subsequent differentiation in the male or the female direction. This fact affords a basis for a critical review of the notion of the indifferent period of gonad formation in fishes, and particularly, the length of that period.

In the analysis of data on the "sensitivity" of germ cells of males to radiation effects, a gradual enhancement of this is manifested in gonia of later orders. For example, in pink salmon, irradiation in the later stages may lead to almost total sterilisation, whereas when embryos were irradiated in the earlier stages, the testes of the experimental fishes were indistinguishable from those of the control group in terms of the number of germ cells, or the number of gonia may even have been slightly greater. Such an increase in the "sensitivity" of the gonia in the course of gametogenesis can be regarded as a consequence of the enhancement in the degree of their sexual directivity. From this point of view, in the gonia of the first cell generations development in the male direction is relatively less pronounced than it is in the gonia of the subsequent generation. It is probable that the transition to meiosis only becomes possible for those germ cells which have achieved a certain degree of sexualisation, and consequently, is normally ruled out for gonia of earlier orders. Here, 104
neurohormonal factors must play a major role as regulators, since the conclusion of the sex differentiation process signifies a new stage in the development of the organism, and for germ cells it denotes the transition to the definitive condition.

The number of mitotic cycles in the early period of gametogenesis - namely the sex differentiation process - is of major importance in the establishing of individual fecundity. This can be most clearly traced in fishes with a monocyclic type of reproduction. The fecundity of which the fishes are capable (potential fecundity) and that which is actually observed in them (ultimate fecundity) do not coincide in their own indices. The former may greatly surpass the latter. The degree of divergence

between the potential and ultimate fecundities in fishes of monocyclic species depends in large measure on the degree of intensity of the process of degeneration of the "surplus" oocytes.

Gaining a more profound understanding of the mechanisms regulating the fecundity of fishes is intimately linked to resolving the problem of the reserve stock of germ cells - its formation, expenditure and replenishment. The existence of such a stock, being a derivative of the functioning of the reproductive system, ensures on the one hand that there is a substantial reserve of germ cells, exceeding "current" requirements, and on the other - the presence of not one, but several paths, thereby providing for a stabilisation or increase in the reproductive capacity of the population (Persov, 1972).

We fully concur with the view of Yu.Yu. Marti (1968) that "surplus fecundity" is not the only method of solving the problem of the reproductive capacity of a population. However, by "surplus fecundity", or as it is defined in the present work, potential fecundity,* the preconditions are created for a rapid response type of reaction to the unfavourable conditions affecting the existence of a population. A trend of this kind can be accomplished by a change in the indices of fecundity of the brood stock or be manifested solely as a temporary interruption of gametogenesis with a subsequent return to normal. In the latter case, the detection of it is linked to a careful study of the process of development of the gonads.

As demonstrated in the present work, the effect of low doses of ionizing radiation can be helpful not only in characterising

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*The two notions are analagous to "the principle of surplus control elements" and fit within the broader concept of the reliability of biological systems (Myakosyan, 1970).

the condition of the reproductive system, but also in studying the problem of growth. In Tilapia mossambica Peters it proved possible to separate the phenomena of reproduction and growth (Fam Man Chung, 1970), that is, to gain the advantage in one process or the other. We have also derived 105
some data on radio stimulation of growth in Atlantic salmon and sturgeon fingerlings (unpublished). This serves as justification for the staging of a series of experiments, both in a laboratory setting and on a semi-industrial scale, not only on aquarium dwellers but also on valuable commercial targets.

Elaboration of the radio stimulation problem may prove to be of far reaching importance, for example in the management of fishes in ponds, where a necessity may arise for establishing a brood stock or for increasing the coefficient of yield of the output for sale, in which the main indices of the efficiency of effort will accordingly be the rate of maturation or the growth rate.

* * *

It stands to reason that the tempting idea of regulating the sex of fishes will require first and foremost a knowledge of the process whereby sex evolves and of its differentiation. As is the case in the majority of animals, the sex of fishes is determined at the moment of fusion of the gametes. In this respect the fishes display a uniformity, as there are no other known methods of determining their sex.

Much more complex is the matter of sex differentiation, since in fishes a wide diversity of ways and means of accomplishing anatomical and cytological differentiation of the gonads in the direction of the ovaries and testes is observed. Therefore, the problem of regulating the sex

differentiation process should be resolved in conformity with and on the basis of a study of the course of development of the reproductive system in expressly one species of fish.

There can be no question that the solving of the sex differentiation problem is of major importance from the standpoint of obtaining an understanding of the mechanisms regulating individual fecundity, and consequently, of developing techniques for controlling the reproductive capacity of a population, which is one of the factors determining the population dynamics of fishes.

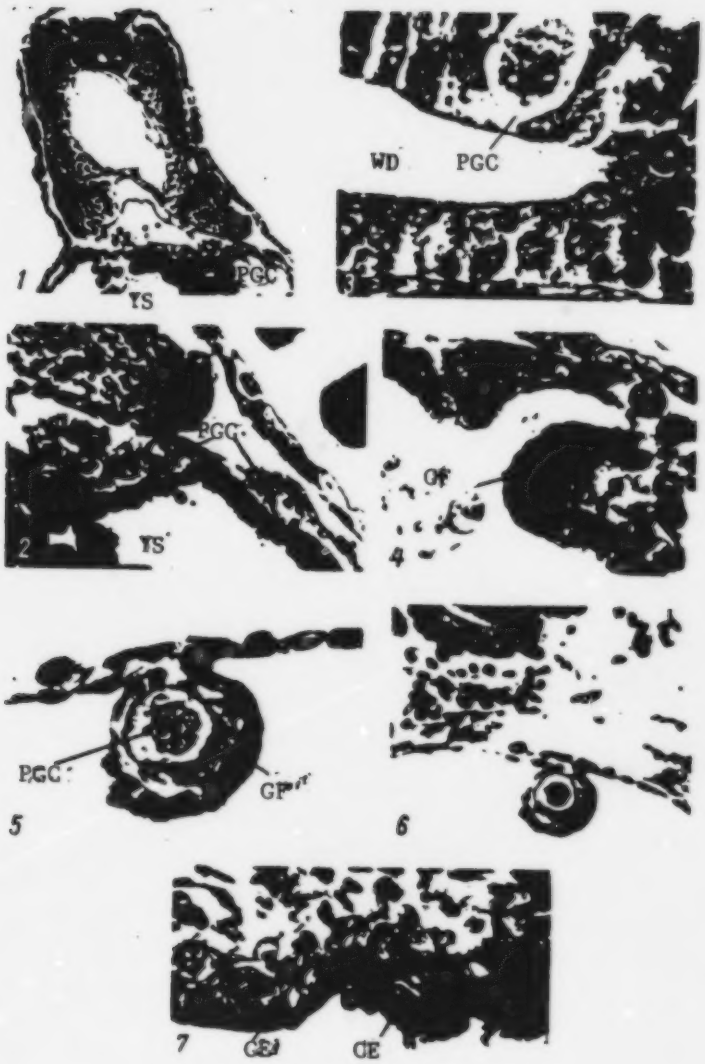


Plate I. Primordial germ cells and gonad establishment in fishes

1 - Primordial germ cells (PGC) during the period of migration into the lateral region of the splanchnotomes. Content of the yolk sac (YS) is in the form of separate clumps. Transverse section. Vimba at time of hatching. Tome fish hatchery, Latviam SSR, 1951. Specimen taken from the collection of O.F. Sakun.

2 - The same, at a higher magnification.

3 - Disintegrating PGC in the wall of a Wolffian duct (WD). 10-day old Baltic salmon larva, length 18 mm, weight 115 mg. April 9, 1964.

4 - Genital fold (GF). Transverse section. Sterlet, 33 days, 33 mm, 200 mg.

5 - PGC in a genital fold in process of formation. Transverse section. Sterlet, 67 days, 75 mm, 2.22 g.

6 - The same at a lower magnification.

7 - Coelomic epithelium (CE) with cilia; germinal epithelium (GE) without cilia. Sterlet, 7.5 months, 10.5 cm, 5.5 g.

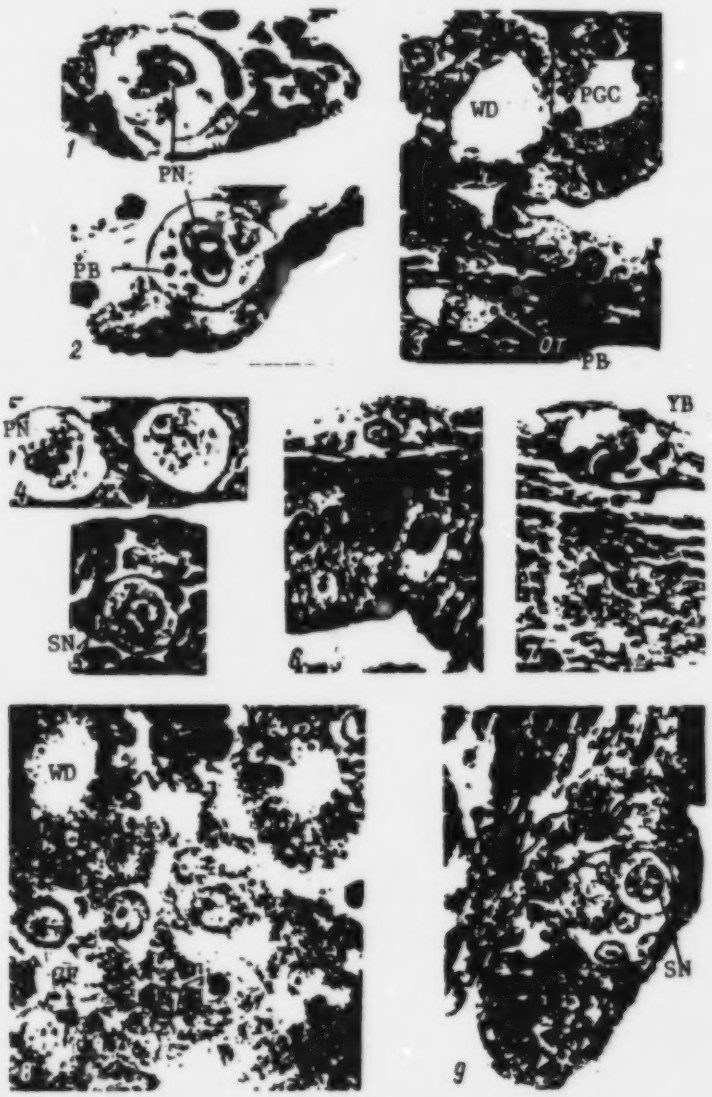


Plate II. Primordial germ cells during period of concentration and transformation of the shape of their nuclei

1,2,3 - polymorphous nuclei (PN) and "perinuclear bodies" (PB) of PGCs. Volga sturgeon, 32 days, 1 g.

4 - PGCs with polymorphous nuclei. Baltic salmon, 10 days, 16 mm, 100 mg. Narva hatchery, April 9, 1958.

5 - PGC with spherical nucleus (SN), shortly before the onset of mitotic divisions. Baikal sturgeon, 34 days, 37 mm, 300 mg.

6 - Individual clumps of yolk in the cytoplasm of a PGC. Transverse section. Baikal sturgeon, 2-3 days, 12.5 mm, 15 mg.

7 - A PGC, the nucleus of which is partly obscured by yolk bodies (YB). Longitudinal section. Lena sturgeon, 1.5 days, 11 mm, 14 mg.

8 - PGCs concentrated in the region of the Wolffian ducts. Pink salmon embryo, 15 days, 157-190 mg. Southern Sakhalin, September 6, 1960.

9 - PGC with spherical nucleus. Hybrid (sturgeon X sterlet), 56 days, 38mm.

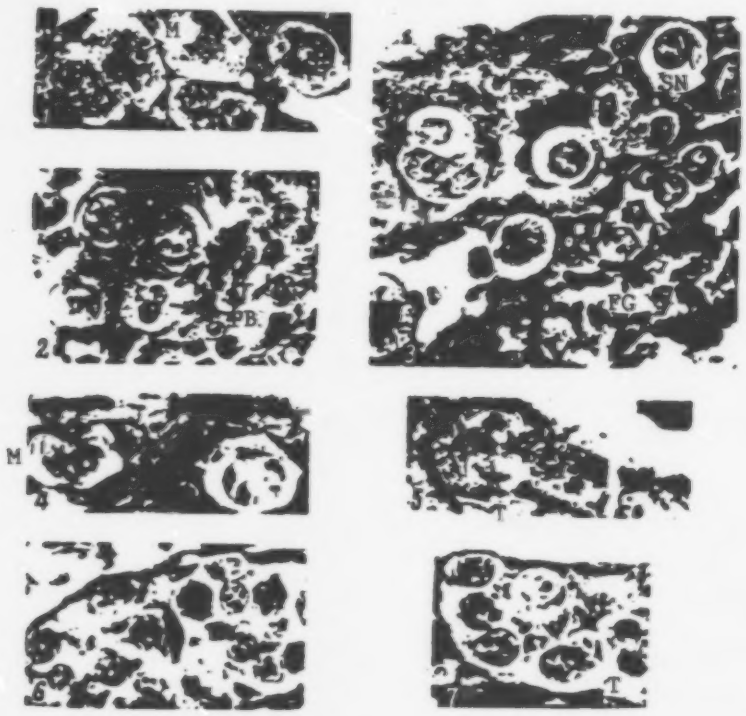


Plate III. Mitotic divisions of primordial germ cells and first-order gonia

1 - metaphase (M) of the division of a PGC. Pink salmon embryo, 18 days, 152-182 mg. Southern Sakhalin, October 4, 1962.

2 - PGC with polymorphous nucleus. Pink salmon embryo, 21 days, 150-185 mg. Southern Sakhalin, October 4, 1962.

3 - PGCs with spherical and polymorphous nuclei. First-order gonia (FG). Pink salmon embryo, 19 days, 136 mg. Arctic.

4 - Metaphase of a PGC. Chum embryo, 45 days. Southern Sakhalin, September 25, 1959.

5 - Telophase (T). Atlantic salmon, 79 days, June 11, 1960.

6,7 - Intensive reproduction of gonia. Pink salmon, S. Sakhalin, November 11, 1958 and October 9, 1959.

Plate IV. Germ cells of salmonid fishes at time of hatching

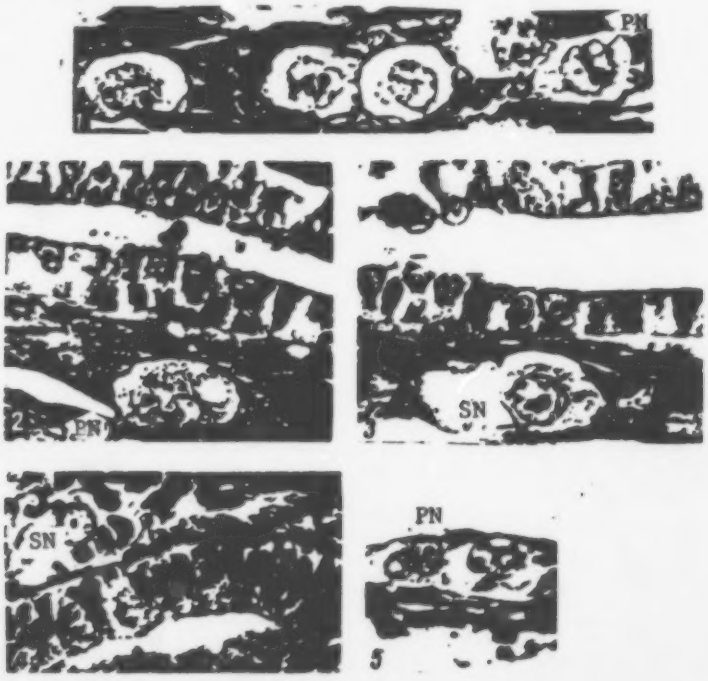
136

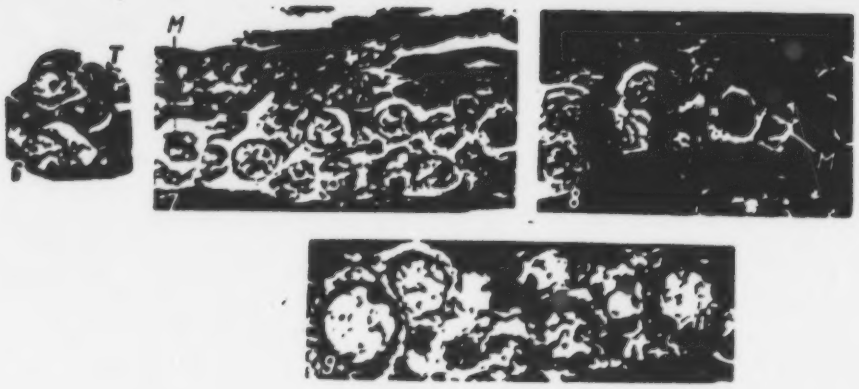
1 - PGCs with nuclei in a polymorphous condition. Atlantic salmon, 30 days, 20 mm, 127 mg. Arctic, May 11, 1960.

2,3 - PGCs with polymorphous and spherical nuclei. Lake trout at time of hatching, 17 mm, 7 mg.

4 - PGC with spherical nucleus. Nelma at time of hatching, 11 mm, 9.5 mg.

5 - PGCs with polymorphous nuclei. Lake salmon, 1 day, 15 mm, 11 mg. Svirskii hatchery, May 12, 1960.





6 - Telophase of a PGC. Coho salmon, 1-2 days, 11-12 mm, 87-98 mg. Kamchatka.

7,8 - Mitotic divisions of gonia of various orders. Sockeye at time of hatching, 22 mm, 110 mg. Kamchatka. Atlantic salmon at time of hatching, 20 mm, 158 mg. S. Sakhalin, August 19, 1960.

9 - Oocytes of diplotene stage prior to beginning of protoplasmic growth. Pink salmon at time of hatching. S. Sakhalin.

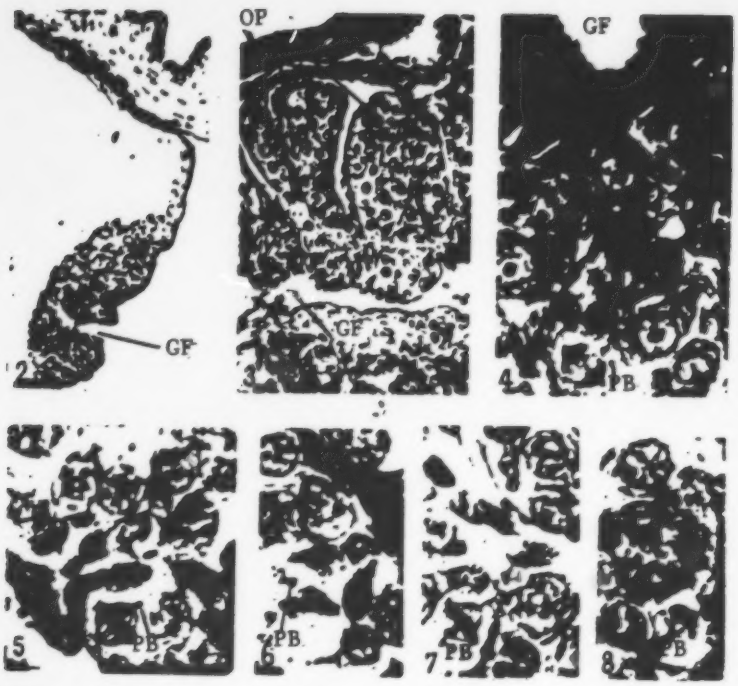
Plate V. Indices of anatomical differentiation of a gonad in the direction of the ovary

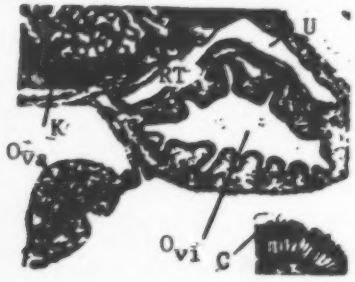
1 - groove-fissure (GF) (whole specimen). Sterlet, 10 months, 16.5 cm, 9.7 g. 137

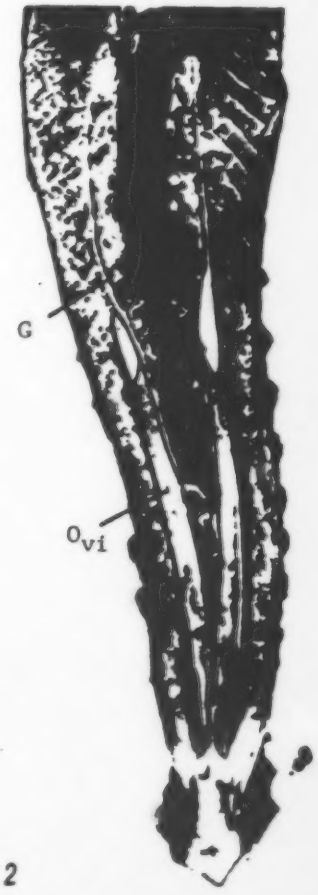
2 - groove-fissure. Transverse section of gonad. Sterlet, 7 months, 16.5 cm, 14.5 g.

3 - groove-fissure in oviferous plates (OP), arranged perpendicularly to it. Sterlet, 30 months, 34 cm, 132 g.

4,5,6,7,8 - active reproduction of oogonia at the time of formation of the groove-fissure. Perinuclear bodies at one of the poles of the mitotic figures (4 - sterlet, 7 months, 16.5 cm, 14.5 g; 5-8 - Baikal sturgeon, 34.2 cm, 107 g).







138

Plate VI. Topography of organs of the urogenital system of juvenile sturgeon and salmonid fishes

1 - kidney (K), renal tubules (RT) flowing into the ureter (U), oviduct (Ovi), ovary (Ova). At lower right corner, part of oviduct of a sexually mature sterlet; epithelial cells with cilia (C). Sterlet, 5.5 months, 15 cm, 8 g.

2 - Gonads (G) and their lateral oviducts (Ovi). "Persian sturgeon", 2 months, 7.9 cm, 2.45 g.

3 - Position and dimensions of right and left ovaries (left is smaller) with oocytes of the protoplasmic growth period. Pink salmon, 75 days, 36 mm, 1950 mg.

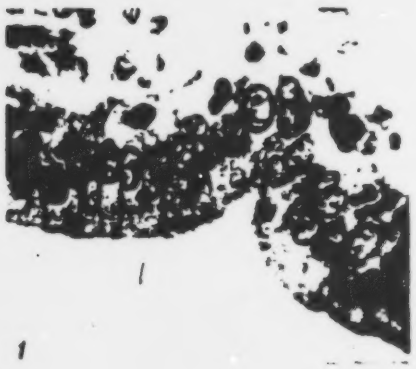
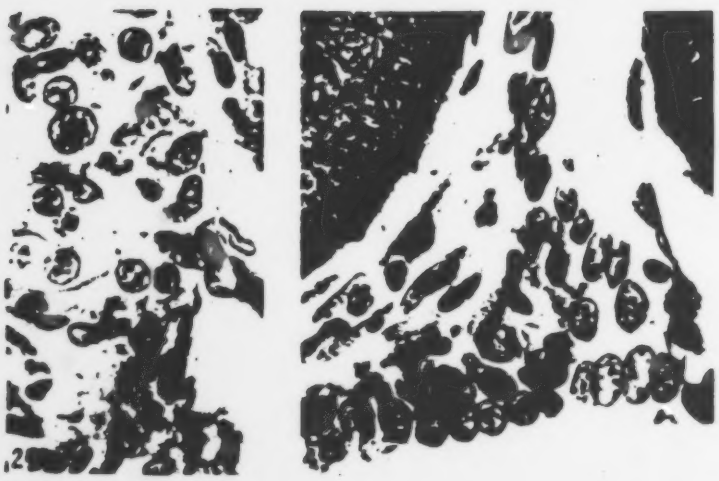


Plate VII Migration of cells of the germinal epithelium into the stroma of the ovary

1,2,4 - beginning of migration of cells of the germinal epithelium. Hybrid (sterlet X sturgeon), caught in the Kama River, 3 years, 55 cm, 490 g.



3 - The same hybrid. "Nest" of oogonia, formed on account of the migrating cells of the germinal epithelium.

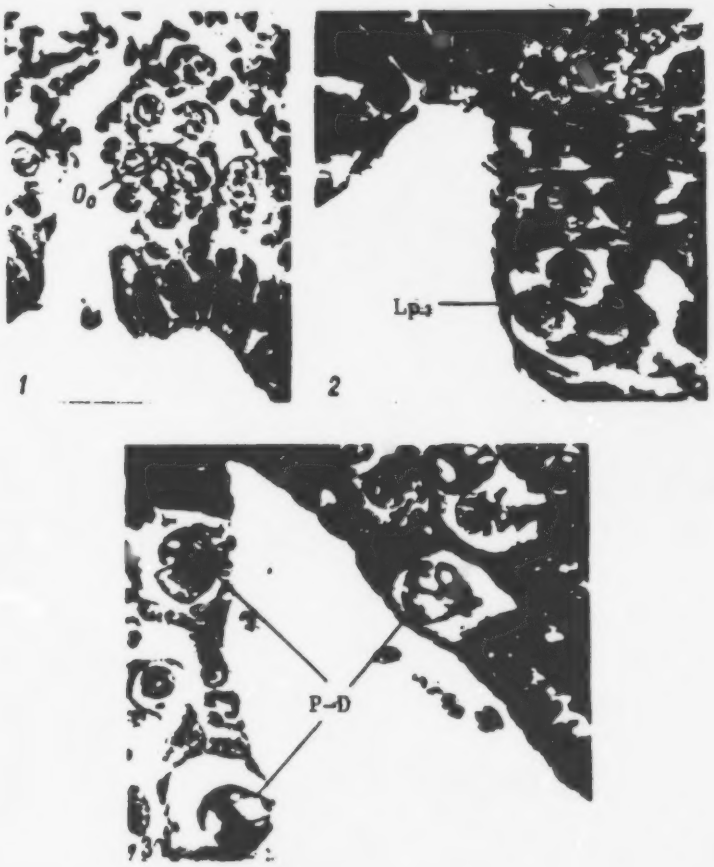
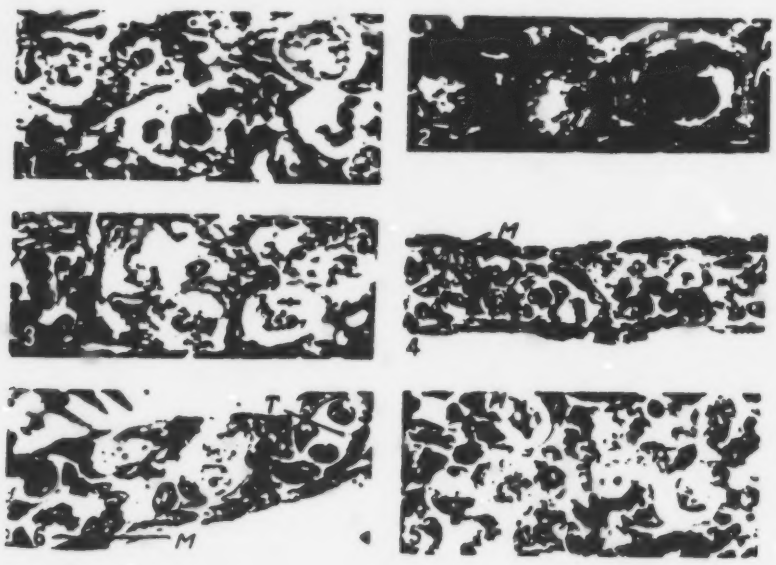


Plate VIII Development of oocytes among the cells of the germinal epithelium

1 - concentration of oogonia (Oo). Sterlet, 5.5 months, 15 cm, 10 g. Female in period of anatomical sex differentiation. Transverse section.

2 - "Nest" of oocytes of the leptotene stage (Lp). Sterlet, 5.5 months, 15 cm, 8 g.

3 - Oocytes of the pachytene-diplotene stage (P-D) among cells of the germinal epithelium bordering the groove-fissure.



141

Plate IX Redifferentiation of ovary to testis in a pink salmon

1 - Total degeneration of oocytes. Pink salmon, 3 months, 28 mm, 195 mg. Arctic. March 10, 1960.

2 - Degeneration of diplotene stage oocytes. Pink salmon, 3 months, 28 mm, 175 mg. Arctic.

3 - Mass degeneration of oocytes. Pink salmon, 5 months, 31 mm, 165 mg. Arctic. April 8, 1960.

4,5 - Total degeneration of oocytes. Mitotic divisions of spermatogonia (4 - pink salmon, 38 days, 18 mm, 73 mg. 5 - pink salmon, 22 mm, 100 mg). Laboratory, December 13, 1964.

6 - Wave of mitotic divisions of spermatogonia after total degeneration of oocytes. Pink salmon, 5 months, 33 mm, 205 mg.

142

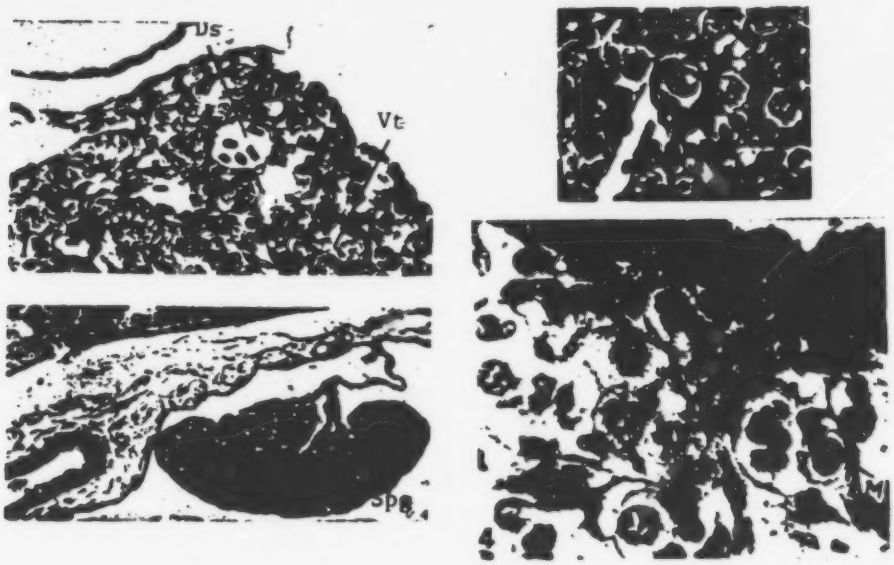
Plate X Anatomical and cytological redifferentiation of an ovary into a testis of a loach

1 - Parovarian cavity (PC) between the ovary and the wall of the trunk. Loach, 7.5 months, 9 cm, 1.5 g.

2,3,4 - Gradual disappearance of parovarian cavity (2 - loach, 8.5 months, 9 cm, 3.6 g; 3 - 7.5 months, 10.5 cm, 7.5 g; 4 - 6.5 months, 9.5 cm, 3.3 g).

5,6 - Total degeneration of oocytes. Together with the degeneration the formation of a testis is occurring. Spermatogonia are clearly visible (5 - loach, 7 months, 8 cm, 2.5 g.; 6 - 6.5 months, 7.5 cm, 1.6 g.).

7 - Spermatogonia (Spg), spermatocytes (Spc), spermatids (Spt). Loach, 6.5 months, 9.5 cm, 3.3 g.



143

Plate XI Anatomical signs of differentiation of a gonad in the direction of a testis

1 - Period of testis formation. Germ cells closer to ventral (Vt) side and blood vessels closer to dorsal (Ds) side of organ. Atlantic salmon from ponds of Pelchi hatchery, 83 days, 5.5 cm, 1.5 g.

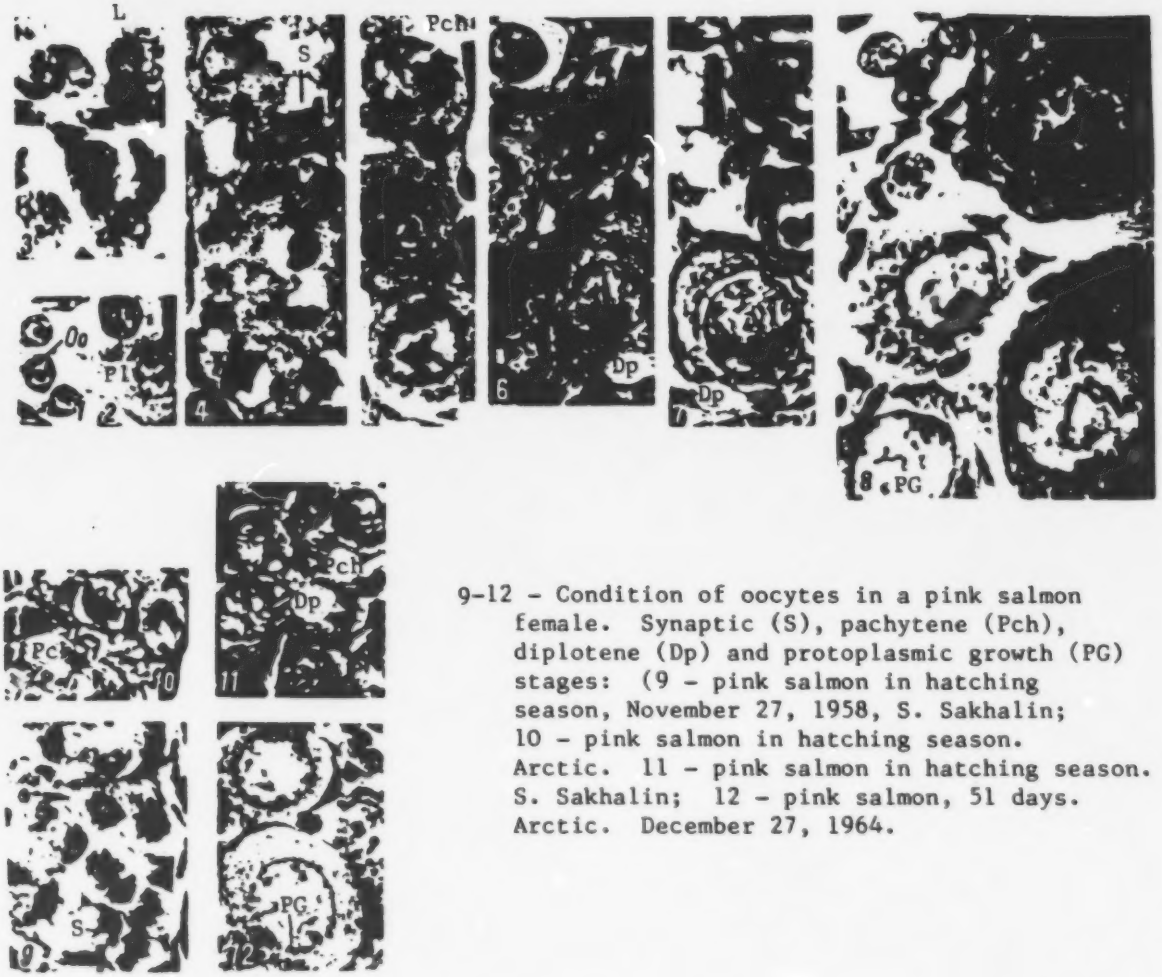
2,3 - Blood vessels in zone of hilus a (2). Spermatogonia (Spg) (3). Transverse section. Baltic salmon, 326 days, 10 cm, 85 g.

4 - Ampullae (Am) in process of formation. Sterlet from Northern Dvina, 55 cm, 600 g.

Plate XII Development of germ cells in an ovary from oogonia to oocytes of protoplasmic growth

144

1 - 8 - Condition of germ cells in salmonid females. Oogonia (Oo) after mitotic division: oogonia during period of transition to oocytes, preleptotene (Pl) and leptotene (L) stages; oocytes of synaptic (S), pachytene (Pch), diplotene (Dp) and protoplasmic growth (PG) stages. (1,5,8 - sterlet, 28 months, 35 cm, 127 g.; 2,3 - Baikal sturgeon, 16.5 months, 35 cm, 120 g.. length of gonads 7 cm, weight of gonads 21 g.; 4 - Ob'sturgeon, 26 months, 47.5 cm, 345 g.; 6 - Northern Dvina sterlet, 38 cm, 200 g.; 7 - Lena sturgeon, 23 months, 30.5 cm, 90 g.).



9-12 - Condition of oocytes in a pink salmon female. Synaptic (S), pachytene (Pch), diplotene (Dp) and protoplasmic growth (PG) stages: (9 - pink salmon in hatching season, November 27, 1958, S. Sakhalin; 10 - pink salmon in hatching season. Arctic. 11 - pink salmon in hatching season. S. Sakhalin; 12 - pink salmon, 51 days. Arctic. December 27, 1964.

Plate XIII First and second stages of development of oocytes of the protoplasmic growth period

1 - 1st stage of protoplasmic growth of oocytes. Pink salmon, 58 days, 21 mm, 105 mg. Arctic, December 20, 1964. 145

2 - 2nd stage of protoplasmic growth of oocytes. Pink salmon, 29 mm, 125 mg, smoltification already completed. Arctic. April 10, 1963.

3 - Same "Lampbrush type" (LB) chromosomes. Pink salmon, 50 days, 35 mm, 236 mg. Laboratory.

4 - Distinctly contoured formation (CF), obtained during special processing for RNA. Pink salmon, 11 months, 15.7 cm. Fixed in Serra* liquid (gallocyanine with naphthalene yellow staining).

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*Transliterated from the Cyrillic. Not found in any reference work consulted. (Tr.).

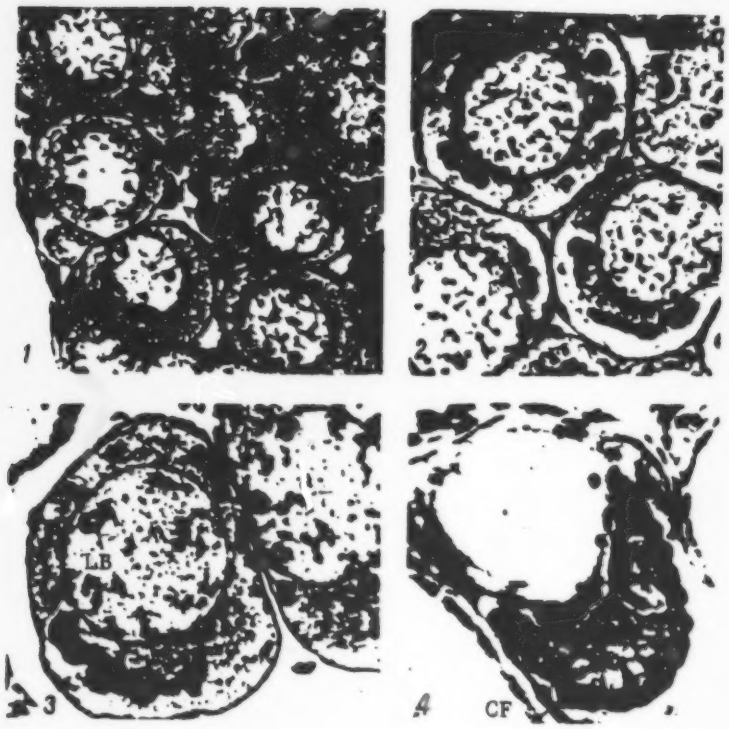
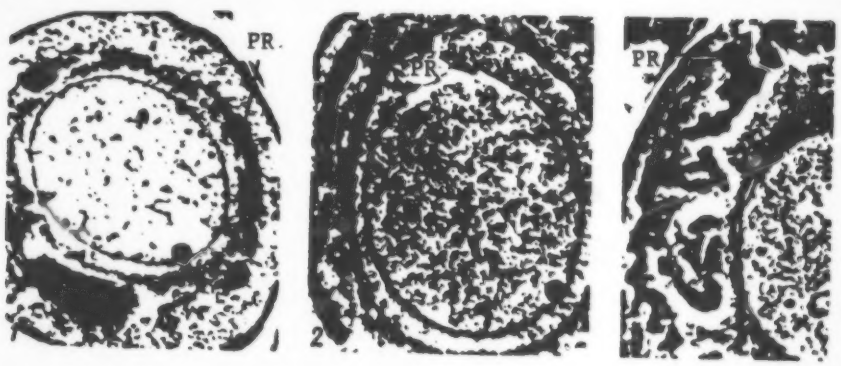
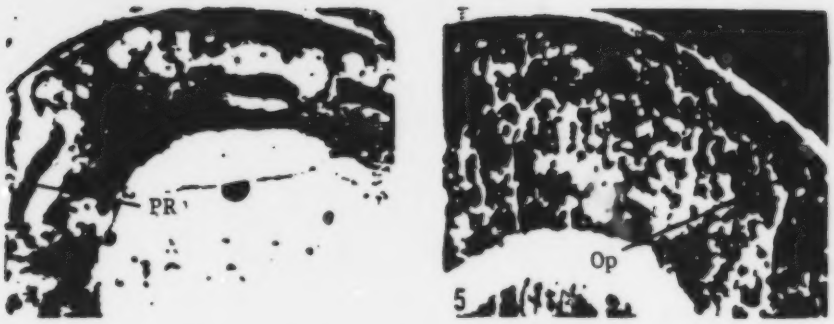


Plate XIV Third stage of development of oocytes of the protoplasmic growth period



1,2,3 - "peripheral ring" (PR) (1 - coho, 6.5 months, 8.7 cm, 6.6 g.; 2 - pink salmon, 5 months. Arctic, June 7, 1960. 3 - chum, 9 months, 7.5 cm, 3.35 g.).

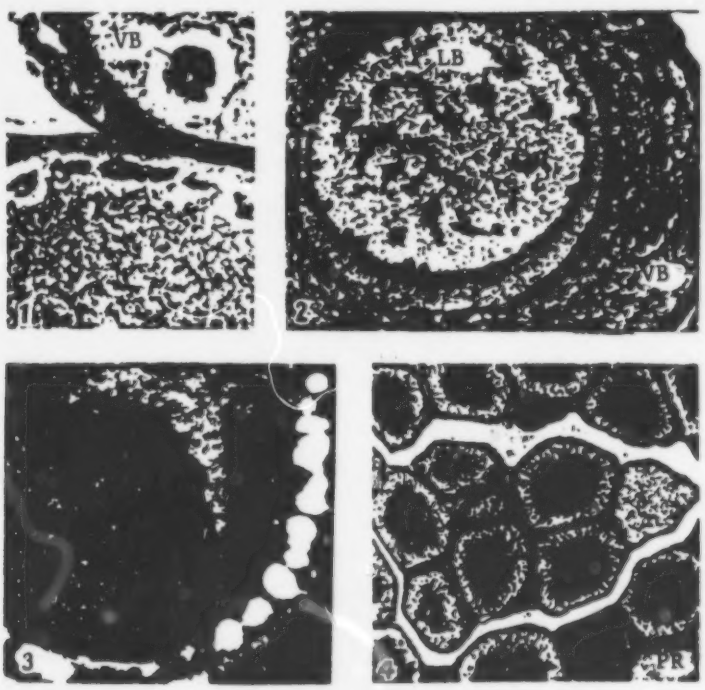


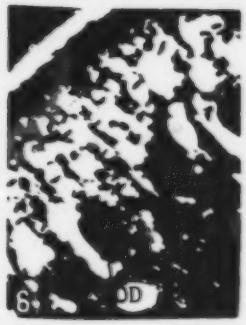
4 - "peripheral ring of an oocyte during processing for RNA. Pink salmon, 10 months, 7.1 cm, 1.72 g. Fixed in Serra liquid, gallocyanine with naphthalene yellow staining.

5 - Small osmiophilous granules (OP). Pink salmon, 10 months, 11.1 cm, 6.8 g.

Plate XV Fourth and fifth stages of development of oocytes of the protoplasmic growth period

147





1 - Peripheral regions of two oocytes. "Peripheral ring" and vitelline body (VB). Pink salmon, 10 months, 11.1 cm, 6.8 g. Arctic. October 15, 1963.

2 - Remains of vitelline body. "Lampbrush type" chromosomes (LB), minute nucleoli. Pink salmon, 5.3 cm, 900 mg. Arctic.

3 - One row of vacuoli along the periphery of the oocytes. Juvenile sockeye during river migration season. Age 2.5 years, 18.5 cm, 34.6 g. Kamchatka.

4 - Heavily vacuolised cytoplasm of oocytes. Remains of "peripheral ring". Pink salmon, 9 months, 11.8 cm, 8.1 g. Arctic. October 31, 1961.

5 - Concentrations of fat droplets (FD) in cytoplasm of oocytes, especially in the perinuclear zone. Pink salmon, 19.5 cm, 75 g. Sea of Japan, Il'insk area, September 27, 1956.

6 - Large osmiophilous droplets (OP). Compressed content of vacuoli. Fixed in osmic acid. Pink salmon, 10 months, 16 cm.

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